



International Institute for  
Applied Systems Analysis  
Schlossplatz 1  
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342  
Fax: +43 2236 71313  
E-mail: [publications@iiasa.ac.at](mailto:publications@iiasa.ac.at)  
Web: [www.iiasa.ac.at](http://www.iiasa.ac.at)

---

## Interim Report

IR-07-050

### Joint Evolution of Predator Body Size and Prey-Size Preference

Tineke Troost ([tineke@bio.vu.nl](mailto:tineke@bio.vu.nl))  
Bob Kooi ([kooi@bio.vu.nl](mailto:kooi@bio.vu.nl))  
Ulf Dieckmann ([dieckmann@iiasa.ac.at](mailto:dieckmann@iiasa.ac.at))

---

#### Approved by

Leen Hordijk  
Director, IIASA

December 2007

---

*Interim Reports* on work of the International Institute for Applied Systems Analysis receive only limited review. Views or opinions expressed herein do not necessarily represent those of the Institute, its National Member Organizations, or other organizations supporting the work.



The Evolution and Ecology Program at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Evolution and Ecology Program brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is collected in the IIASA Studies in Adaptive Dynamics series.

- No. 1 Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS: *Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction*. IIASA Working Paper WP-95-099 (1995). van Strien SJ, Verduyn Lunel SM (eds): *Stochastic and Spatial Structures of Dynamical Systems*, Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen), North Holland, Amsterdam, pp. 183-231 (1996).
- No. 2 Dieckmann U, Law R: *The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes*. IIASA Working Paper WP-96-001 (1996). *Journal of Mathematical Biology* 34:579-612 (1996).
- No. 3 Dieckmann U, Marrow P, Law R: *Evolutionary Cycling of Predator-Prey Interactions: Population Dynamics and the Red Queen*. IIASA Preprint (1995). *Journal of Theoretical Biology* 176:91-102 (1995).
- No. 4 Marrow P, Dieckmann U, Law R: *Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective*. IIASA Working Paper WP-96-002 (1996). *Journal of Mathematical Biology* 34:556-578 (1996).
- No. 5 Law R, Marrow P, Dieckmann U: *On Evolution under Asymmetric Competition*. IIASA Working Paper WP-96-003 (1996). *Evolutionary Ecology* 11:485-501 (1997).
- No. 6 Metz JAJ, Mylius SD, Diekmann O: *When Does Evolution Optimize? On the Relation Between Types of Density Dependence and Evolutionarily Stable Life History Parameters*. IIASA Working Paper WP-96-004 (1996).
- No. 7 Ferrière R, Gatto M: *Lyapunov Exponents and the Mathematics of Invasion in Oscillatory or Chaotic Populations*. *Theoretical Population Biology* 48:126-171 (1995).
- No. 8 Ferrière R, Fox GA: *Chaos and Evolution*. IIASA Preprint (1996). *Trends in Ecology and Evolution* 10:480-485 (1995).
- No. 9 Ferrière R, Michod RE: *The Evolution of Cooperation in Spatially Heterogeneous Populations*. IIASA Working Paper WP-96-029 (1996). *The American Naturalist* 147:692-717 (1996).
- No. 10 van Dooren TJM, Metz JAJ: *Delayed Maturation in Temporally Structured Populations with Non-Equilibrium Dynamics*. IIASA Working Paper WP-96-070 (1996). *Journal of Evolutionary Biology* 11:41-62 (1998).
- No. 11 Geritz SAH, Metz JAJ, Kisdi É, Meszéna G: *The Dynamics of Adaptation and Evolutionary Branching*. IIASA Working Paper WP-96-077 (1996). *Physical Review Letters* 78:2024-2027 (1997).
- No. 12 Geritz SAH, Kisdi É, Meszéna G, Metz JAJ: *Evolutionary Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree*. IIASA Working Paper WP-96-114 (1996). *Evolutionary Ecology* 12:35-57 (1998).
- No. 13 Heino M, Metz JAJ, Kaitala V: *Evolution of Mixed Maturation Strategies in Semelparous Life-Histories: The Crucial Role of Dimensionality of Feedback Environment*. IIASA Working Paper WP-96-126 (1996). *Philosophical Transactions of the Royal Society of London Series B* 352:1647-1655 (1997).
- No. 14 Dieckmann U: *Can Adaptive Dynamics Invade?* IIASA Working Paper WP-96-152 (1996). *Trends in Ecology and Evolution* 12:128-131 (1997).
- No. 15 Meszéna G, Czibula I, Geritz SAH: *Adaptive Dynamics in a 2-Patch Environment: A Simple Model for Allopatric and Parapatric Speciation*. IIASA Interim Report IR-97-001 (1997). *Journal of Biological Systems* 5:265-284 (1997).
- No. 16 Heino M, Metz JAJ, Kaitala V: *The Enigma of Frequency-Dependent Selection*. IIASA Interim Report IR-97-061 (1997). *Trends in Ecology and Evolution* 13:367-370 (1998).
- No. 17 Heino M: *Management of Evolving Fish Stocks*. IIASA Interim Report IR-97-062 (1997). *Canadian Journal of Fisheries and Aquatic Sciences* 55:1971-1982 (1998).
- No. 18 Heino M: *Evolution of Mixed Reproductive Strategies in Simple Life-History Models*. IIASA Interim Report IR-97-063 (1997).
- No. 19 Geritz SAH, van der Meijden E, Metz JAJ: *Evolutionary Dynamics of Seed Size and Seedling Competitive Ability*. IIASA Interim Report IR-97-071 (1997). *Theoretical Population Biology* 55:324-343 (1999).
- No. 20 Galis F, Metz JAJ: *Why Are There So Many Cichlid Species? On the Interplay of Speciation and Adaptive Radiation*. IIASA Interim Report IR-97-072 (1997). *Trends in Ecology and Evolution* 13:1-2 (1998).

- No. 21 Boerlijst MC, Nowak MA, Sigmund K: *Equal Pay for all Prisoners/ The Logic of Contrition*. IIASA Interim Report IR-97-073 (1997). American Mathematical Society Monthly 104:303-307 (1997). Journal of Theoretical Biology 185:281-293 (1997).
- No. 22 Law R, Dieckmann U: *Symbiosis Without Mutualism and the Merger of Lineages in Evolution*. IIASA Interim Report IR-97-074 (1997). Proceedings of the Royal Society of London Series B 265:1245-1253 (1998).
- No. 23 Klinkhamer PGL, de Jong TJ, Metz JAJ: *Sex and Size in Cosexual Plants*. IIASA Interim Report IR-97-078 (1997). Trends in Ecology and Evolution 12:260-265 (1997).
- No. 24 Fontana W, Schuster P: *Shaping Space: The Possible and the Attainable in RNA Genotype-Phenotype Mapping*. IIASA Interim Report IR-98-004 (1998). Journal of Theoretical Biology 194:491-515 (1998).
- No. 25 Kisdi É, Geritz SAH: *Adaptive Dynamics in Allele Space: Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment*. IIASA Interim Report IR-98-038 (1998). Evolution 53:993-1008 (1999).
- No. 26 Fontana W, Schuster P: *Continuity in Evolution: On the Nature of Transitions*. IIASA Interim Report IR-98-039 (1998). Science 280:1451-1455 (1998).
- No. 27 Nowak MA, Sigmund K: *Evolution of Indirect Reciprocity by Image Scoring/ The Dynamics of Indirect Reciprocity*. IIASA Interim Report IR-98-040 (1998). Nature 393:573-577 (1998). Journal of Theoretical Biology 194:561-574 (1998).
- No. 28 Kisdi É: *Evolutionary Branching Under Asymmetric Competition*. IIASA Interim Report IR-98-045 (1998). Journal of Theoretical Biology 197:149-162 (1999).
- No. 29 Berger U: *Best Response Adaptation for Role Games*. IIASA Interim Report IR-98-086 (1998).
- No. 30 van Dooren TJM: *The Evolutionary Ecology of Dominance-Recessivity*. IIASA Interim Report IR-98-096 (1998). Journal of Theoretical Biology 198:519-532 (1999).
- No. 31 Dieckmann U, O'Hara B, Weisser W: *The Evolutionary Ecology of Dispersal*. IIASA Interim Report IR-98-108 (1998). Trends in Ecology and Evolution 14:88-90 (1999).
- No. 32 Sigmund K: *Complex Adaptive Systems and the Evolution of Reciprocation*. IIASA Interim Report IR-98-100 (1998). Ecosystems 1:444-448 (1998).
- No. 33 Posch M, Pichler A, Sigmund K: *The Efficiency of Adapting Aspiration Levels*. IIASA Interim Report IR-98-103 (1998). Proceedings of the Royal Society London Series B 266:1427-1435 (1999).
- No. 34 Mathias A, Kisdi É: *Evolutionary Branching and Coexistence of Germination Strategies*. IIASA Interim Report IR-99-014 (1999).
- No. 35 Dieckmann U, Doebeli M: *On the Origin of Species by Sympatric Speciation*. IIASA Interim Report IR-99-013 (1999). Nature 400:354-357 (1999).
- No. 36 Metz JAJ, Gyllenberg M: *How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies*. IIASA Interim Report IR-99-019 (1999). Proceedings of the Royal Society of London Series B 268:499-508 (2001).
- No. 37 Gyllenberg M, Metz JAJ: *On Fitness in Structured Metapopulations*. IIASA Interim Report IR-99-037 (1999). Journal of Mathematical Biology 43:545-560 (2001).
- No. 38 Meszéna G, Metz JAJ: *Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality*. IIASA Interim Report IR-99-045 (1999).
- No. 39 Kisdi É, Geritz SAH: *Evolutionary Branching and Sympatric Speciation in Diploid Populations*. IIASA Interim Report IR-99-048 (1999).
- No. 40 Ylikarjula J, Heino M, Dieckmann U: *Ecology and Adaptation of Stunted Growth in Fish*. IIASA Interim Report IR-99-050 (1999). Evolutionary Ecology 13:433-453 (1999).
- No. 41 Nowak MA, Sigmund K: *Games on Grids*. IIASA Interim Report IR-99-038 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 135-150 (2000).
- No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation*. IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).
- No. 43 Kisdi É, Jacobs FJA, Geritz SAH: *Red Queen Evolution by Cycles of Evolutionary Branching and Extinction*. IIASA Interim Report IR-00-030 (2000). Selection 2:161-176 (2001).
- No. 44 Meszéna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ: *Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics*. IIASA Interim Report IR-00-039 (2000). Selection 2:193-210 (2001).
- No. 45 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ: *Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity*. IIASA Interim Report IR-00-035 (2000). Journal of Evolutionary Biology 16:143-153 (2003).
- No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions*. IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).
- No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model*. IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).
- No. 48 Gyllenberg M, Parvinen K, Dieckmann U: *Evolutionary Suicide and Evolution of Dispersal in Structured Metapopulations*. IIASA Interim Report IR-00-056 (2000). Journal of Mathematical Biology 45:79-105 (2002).
- No. 49 van Dooren TJM: *The Evolutionary Dynamics of Direct Phenotypic Overdominance: Emergence Possible, Loss Probable*. IIASA Interim Report IR-00-048 (2000). Evolution 54:1899-1914 (2000).
- No. 50 Nowak MA, Page KM, Sigmund K: *Fairness Versus Reason in the Ultimatum Game*. IIASA Interim Report IR-00-57 (2000). Science 289:1773-1775 (2000).
- No. 51 de Feo O, Ferrière R: *Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling*. IIASA Interim Report IR-00-074 (2000). International Journal of Bifurcation and Chaos 10:443-452 (2000).

- No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola*. IIASA Interim Report IR-01-018 (2001). *Oikos* 94:525-532 (2001).
- No. 53 Sigmund K, Hauert C, Nowak MA: *Reward and Punishment in Minigames*. IIASA Interim Report IR-01-031 (2001). *Proceedings of the National Academy of Sciences of the USA* 98:10757-10762 (2001).
- No. 54 Hauert C, De Monte S, Sigmund K, Hofbauer J: *Oscillations in Optional Public Good Games*. IIASA Interim Report IR-01-036 (2001).
- No. 55 Ferrière R, Le Galliard J: *Invasion Fitness and Adaptive Dynamics in Spatial Population Models*. IIASA Interim Report IR-01-043 (2001). Clobert J, Dhondt A, Danchin E, Nichols J (eds): *Dispersal*, Oxford University Press, pp. 57-79 (2001).
- No. 56 de Mazancourt C, Loreau M, Dieckmann U: *Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism?* IIASA Interim Report IR-01-053 (2001). *The American Naturalist* 158:109-123 (2001).
- No. 57 Claessen D, Dieckmann U: *Ontogenetic Niche Shifts and Evolutionary Branching in Size-Structured Populations*. IIASA Interim Report IR-01-056 (2001). *Evolutionary Ecology Research* 4:189-217 (2002).
- No. 58 Brandt H: *Correlation Analysis of Fitness Landscapes*. IIASA Interim Report IR-01-058 (2001).
- No. 59 Dieckmann U: *Adaptive Dynamics of Pathogen-Host Interactions*. IIASA Interim Report IR-02-007 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 39-59 (2002).
- No. 60 Nowak MA, Sigmund K: *Super- and Coinfection: The Two Extremes*. IIASA Interim Report IR-02-008 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 124-137 (2002).
- No. 61 Sabelis MW, Metz JAJ: *Evolution Management: Taking Stock - Relating Theory to Experiment*. IIASA Interim Report IR-02-009 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 379-398 (2002).
- No. 62 Cheptou P, Dieckmann U: *The Evolution of Self-Fertilization in Density-Regulated Populations*. IIASA Interim Report IR-02-024 (2002). *Proceedings of the Royal Society of London Series B* 269:1177-1186 (2002).
- No. 63 Bürger R: *Additive Genetic Variation Under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study*. IIASA Interim Report IR-02-013 (2002). *Theoretical Population Biology* 61:197-213 (2002).
- No. 64 Hauert C, De Monte S, Hofbauer J, Sigmund K: *Volunteering as Red Queen Mechanism for Co-operation in Public Goods Games*. IIASA Interim Report IR-02-041 (2002). *Science* 296:1129-1132 (2002).
- No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition*. IIASA Interim Report IR-02-053 (2002). *Evolution* 56:1081-1090 (2002).
- No. 66 Dercole F, Rinaldi S: *Evolution of Cannibalistic Traits: Scenarios Derived from Adaptive Dynamics*. IIASA Interim Report IR-02-054 (2002). *Theoretical Population Biology* 62:365-374 (2002).
- No. 67 Bürger R, Gimelfarb A: *Fluctuating Environments and the Role of Mutation in Maintaining Quantitative Genetic Variation*. IIASA Interim Report IR-02-058 (2002). *Genetical Research* 80:31-46 (2002).
- No. 68 Bürger R: *On a Genetic Model of Intraspecific Competition and Stabilizing Selection*. IIASA Interim Report IR-02-062 (2002). *Amer. Natur.* 160:661-682 (2002).
- No. 69 Doebeli M, Dieckmann U: *Speciation Along Environmental Gradients*. IIASA Interim Report IR-02-079 (2002). *Nature* 421:259-264 (2003).
- No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model*. IIASA Interim Report IR-02-078 (2002). *SIAM Journal on Applied Mathematics* 63:1378-1391 (2003).
- No. 71 Le Galliard J, Ferrière R, Dieckmann U: *The Adaptive Dynamics of Altruism in Spatially Heterogeneous Populations*. IIASA Interim Report IR-03-006 (2003). *Evolution* 57:1-17 (2003).
- No. 72 Taborsky B, Dieckmann U, Heino M: *Unexpected Discontinuities in Life-History Evolution under Size-Dependent Mortality*. IIASA Interim Report IR-03-004 (2003). *Proceedings of the Royal Society of London Series B* 270:713-721 (2003).
- No. 73 Gardmark A, Dieckmann U, Lundberg P: *Life-History Evolution in Harvested Populations: The Role of Natural Predation*. IIASA Interim Report IR-03-008 (2003). *Evolutionary Ecology Research* 5:239-257 (2003).
- No. 74 Mizera F, Meszéna G: *Spatial Niche Packing, Character Displacement and Adaptive Speciation Along an Environmental Gradient*. IIASA Interim Report IR-03-062 (2003). *Evolutionary Ecology Research* 5:363-382 (2003).
- No. 75 Dercole F: *Remarks on Branching-Extinction Evolutionary Cycles*. IIASA Interim Report IR-03-077 (2003). *Journal of Mathematical Biology* 47:569-580 (2003).
- No. 76 Hofbauer J, Sigmund K: *Evolutionary Game Dynamics*. IIASA Interim Report IR-03-078 (2003). *Bulletin of the American Mathematical Society* 40:479-519 (2003).
- No. 77 Ernande B, Dieckmann U, Heino M: *Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation*. IIASA Interim Report IR-03-058 (2003). *Proceedings of the Royal Society of London Series B-Biological Sciences* 271:415-423 (2004).
- No. 78 Hanski I, Heino M: *Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes*. IIASA Interim Report IR-03-028 (2003). *Theoretical Population Biology* 63:309-338 (2003).
- No. 79 van Doorn G, Dieckmann U, Weissing FJ: *Sympatric Speciation by Sexual Selection: A Critical Re-Evaluation*. IIASA Interim Report IR-04-003 (2004). *American Naturalist* 163:709-725 (2004).
- No. 80 Egas M, Dieckmann U, Sabelis MW: *Evolution Restricts the Coexistence of Specialists and Generalists - the Role of Trade-off Structure*. IIASA Interim Report IR-04-004 (2004). *American Naturalist* 163:518-531 (2004).

- No. 81 Ernande B, Dieckmann U: *The Evolution of Phenotypic Plasticity in Spatially Structured Environments: Implications of Intraspecific Competition, Plasticity Costs, and Environmental Characteristics*. IIASA Interim Report IR-04-006 (2004). *Journal of Evolutionary Biology* 17:613-628 (2004).
- No. 82 Cressman R, Hofbauer J: *Measure Dynamics on a One-Dimensional Continuous Trait Space: Theoretical Foundations for Adaptive Dynamics*. IIASA Interim Report IR-04-016 (2004).
- No. 83 Cressman R: *Dynamic Stability of the Replicator Equation with Continuous Strategy Space*. IIASA Interim Report IR-04-017 (2004).
- No. 84 Ravigné V, Olivieri I, Dieckmann U: *Implications of Habitat Choice for Protected Polymorphisms*. IIASA Interim Report IR-04-005 (2004). *Evolutionary Ecology Research* 6:125-145 (2004).
- No. 85 Nowak MA, Sigmund K: *Evolutionary Dynamics of Biological Games*. IIASA Interim Report IR-04-013 (2004). *Science* 303:793-799 (2004).
- No. 86 Vukics A, Asbóth J, Meszéna G: *Speciation in Multidimensional Evolutionary Space*. IIASA Interim Report IR-04-028 (2004). *Physical Review* 68:041-903 (2003).
- No. 87 de Mazancourt C, Dieckmann U: *Trade-off Geometries and Frequency-dependent Selection*. IIASA Interim Report IR-04-039 (2004). *American Naturalist* 164:765-778 (2004).
- No. 88 Cadet CR, Metz JAJ, Klinkhamer PGL: *Size and the Not-So-Single Sex: Disentangling the Effects of Size on Sex Allocation*. IIASA Interim Report IR-04-084 (2004). *American Naturalist* 164:779-792 (2004).
- No. 89 Rueffler C, van Dooren TJM, Metz JAJ: *Adaptive Walks on Changing Landscapes: Levins' Approach Extended*. IIASA Interim Report IR-04-083 (2004). *Theoretical Population Biology* 65:165-178 (2004).
- No. 90 de Mazancourt C, Loreau M, Dieckmann U: *Understanding Mutualism When There is Adaptation to the Partner*. IIASA Interim Report IR-05-016 (2005). *Journal of Ecology* 93:305-314 (2005).
- No. 91 Dieckmann U, Doebeli M: *Pluralism in Evolutionary Theory*. IIASA Interim Report IR-05-017 (2005). *Journal of Evolutionary Biology* 18:1209-1213 (2005).
- No. 92 Doebeli M, Dieckmann U, Metz JAJ, Tautz D: *What We Have Also Learned: Adaptive Speciation is Theoretically Plausible*. IIASA Interim Report IR-05-018 (2005). *Evolution* 59:691-695 (2005).
- No. 93 Egas M, Sabelis MW, Dieckmann U: *Evolution of Specialization and Ecological Character Displacement of Herbivores Along a Gradient of Plant Quality*. IIASA Interim Report IR-05-019 (2005). *Evolution* 59:507-520 (2005).
- No. 94 Le Galliard J, Ferrière R, Dieckmann U: *Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility*. IIASA Interim Report IR-05-020 (2005). *American Naturalist* 165:206-224 (2005).
- No. 95 Doebeli M, Dieckmann U: *Adaptive Dynamics as a Mathematical Tool for Studying the Ecology of Speciation Processes*. IIASA Interim Report IR-05-022 (2005). *Journal of Evolutionary Biology* 18:1194-1200 (2005).
- No. 96 Brandt H, Sigmund K: *The Logic of Reprobation: Assessment and Action Rules for Indirect Reciprocity*. IIASA Interim Report IR-04-085 (2004). *Journal of Theoretical Biology* 231:475-486 (2004).
- No. 97 Hauert C, Haiden N, Sigmund K: *The Dynamics of Public Goods*. IIASA Interim Report IR-04-086 (2004). *Discrete and Continuous Dynamical Systems - Series B* 4:575-587 (2004).
- No. 98 Meszéna G, Gyllenberg M, Jacobs FJA, Metz JAJ: *Link Between Population Dynamics and Dynamics of Darwinian Evolution*. IIASA Interim Report IR-05-026 (2005). *Physical Review Letters* 95:Article 078105 (2005).
- No. 99 Meszéna G: *Adaptive Dynamics: The Continuity Argument*. IIASA Interim Report IR-05-032 (2005).
- No. 100 Brännström NA, Dieckmann U: *Evolutionary Dynamics of Altruism and Cheating Among Social Amoebas*. IIASA Interim Report IR-05-039 (2005). *Proceedings of the Royal Society London Series B* 272:1609-1616 (2005).
- No. 101 Meszéna G, Gyllenberg M, Pasztor L, Metz JAJ: *Competitive Exclusion and Limiting Similarity: A Unified Theory*. IIASA Interim Report IR-05-040 (2005).
- No. 102 Szabo P, Meszéna G: *Limiting Similarity Revisited*. IIASA Interim Report IR-05-050 (2005).
- No. 103 Krakauer DC, Sasaki A: *The Greater than Two-Fold Cost of Integration for Retroviruses*. IIASA Interim Report IR-05-069 (2005).
- No. 104 Metz JAJ: *Eight Personal Rules for Doing Science*. IIASA Interim Report IR-05-073 (2005). *Journal of Evolutionary Biology* 18:1178-1181 (2005).
- No. 105 Beltman JB, Metz JAJ: *Speciation: More Likely Through a Genetic or Through a Learned Habitat Preference?* IIASA Interim Report IR-05-072 (2005). *Proceedings of the Royal Society of London Series B* 272:1455-1463 (2005).
- No. 106 Durinx M, Metz JAJ: *Multi-type Branching Processes and Adaptive Dynamics of Structured Populations*. IIASA Interim Report IR-05-074 (2005). Haccou P, Jager P, Vatutin V (eds): *Branching Processes: Variation, Growth and Extinction of Populations*, Cambridge University Press, Cambridge, UK, pp. 266-278 (2005).
- No. 107 Brandt H, Sigmund K: *The Good, the Bad and the Discriminator - Errors in Direct and Indirect Reciprocity*. IIASA Interim Report IR-05-070 (2005). *Journal of Theoretical Biology* 239:183-194 (2006).
- No. 108 Brandt H, Hauert C, Sigmund K: *Punishing and Abstaining for Public Goods*. IIASA Interim Report IR-05-071 (2005). *Proceedings of the National Academy of Sciences of the United States of America* 103:495-497 (2006).
- No. 109 Ohtsuki A, Sasaki A: *Epidemiology and Disease-Control Under Gene-for-Gene Plant-Pathogen Interaction*. IIASA Interim Report IR-05-068 (2005).
- No. 110 Brandt H, Sigmund K: *Indirect Reciprocity, Image-Scoring, and Moral Hazard*. IIASA Interim Report IR-05-078 (2005). *Proceedings of the National Academy of Sciences of the United States of America* 102:2666-2670 (2005).
- No. 111 Nowak MA, Sigmund K: *Evolution of Indirect Reciprocity*. IIASA Interim Report IR-05-079 (2005). *Nature* 437:1292-1298 (2005).
- No. 112 Kamo M, Sasaki A: *Evolution Towards Multi-Year Periodicity in Epidemics*. IIASA Interim Report IR-05-080 (2005). *Ecology Letters* 8:378-385 (2005).

- No. 113 Dercole F, Ferrière R, Gragnani A, Rinaldi S: *Coevolution of Slow-fast Populations: Evolutionary Sliding, Evolutionary Pseudo-equilibria, and Complex Red Queen Dynamics*. IIASA Interim Report IR-06-006 (2006). *Proceedings of the Royal Society B* 273:983-990 (2006).
- No. 114 Dercole F: *Border Collision Bifurcations in the Evolution of Mutualistic Interactions*. IIASA Interim Report IR-05-083 (2005). *International Journal of Bifurcation and Chaos* 15:2179-2190 (2005).
- No. 115 Dieckmann U, Heino M, Parvinen K: *The Adaptive Dynamics of Function-Valued Traits*. IIASA Interim Report IR-06-036 (2006). *Journal of Theoretical Biology* 241:370-389 (2006).
- No. 116 Dieckmann U, Metz JAJ: *Surprising Evolutionary Predictions from Enhanced Ecological Realism*. IIASA Interim Report IR-06-037 (2006). *Theoretical Population Biology* 69:263-281 (2006).
- No. 117 Dieckmann U, Brännström NA, HilleRisLambers R, Ito H: *The Adaptive Dynamics of Community Structure*. IIASA Interim Report IR-06-038 (2006). Takeuchi Y, Iwasa Y, Sato K (eds): *Mathematics for Ecology and Environmental Sciences*, Springer, Berlin Heidelberg, pp. 145-177 (2007).
- No. 118 Gardmark A, Dieckmann U: *Disparate Maturation Adaptations to Size-dependent Mortality*. IIASA Interim Report IR-06-039 (2006). *Proceedings of the Royal Society London Series B* 273:2185-2192 (2006).
- No. 119 van Doorn G, Dieckmann U: *The Long-term Evolution of Multi-locus Traits Under Frequency-dependent Disruptive Selection*. IIASA Interim Report IR-06-041 (2006). *Evolution* 60:2226-2238 (2006).
- No. 120 Doebeli M, Blok HJ, Leimar O, Dieckmann U: *Multimodal Pattern Formation in Phenotype Distributions of Sexual Populations*. IIASA Interim Report IR-06-046 (2006). *Proceedings of the Royal Society London Series B* 274:347-357 (2007).
- No. 121 Dunlop ES, Shuter BJ, Dieckmann U: *The Demographic and Evolutionary Consequences of Selective Mortality: Predictions from an Eco-genetic Model of the Smallmouth Bass*. IIASA Interim Report IR-06-060 (2006). *Transactions of the American Fisheries Society* 136:749-765 (2007).
- No. 122 Metz JAJ: *Fitness*. IIASA Interim Report IR-06-061 (2006).
- No. 123 Brandt H, Ohtsuki H, Iwasa Y, Sigmund K: *A Survey on Indirect Reciprocity*. IIASA Interim Report IR-06-065 (2006). Takeuchi Y, Iwasa Y, Sato K (eds): *Mathematics for Ecology and Environmental Sciences*, Springer, Berlin Heidelberg, pp. 21-51 (2007).
- No. 124 Dercole F, Loiacono D, Rinaldi S: *Synchronization in Ecological Networks: A Byproduct of Darwinian Evolution?* IIASA Interim Report IR-06-068 (2006). *International Journal of Bifurcation and Chaos* 7:2435-2446 (2007).
- No. 125 Dercole F, Dieckmann U, Obersteiner M, Rinaldi S: *Adaptive Dynamics and Technological Change*. IIASA Interim Report IR-06-070 (2006).
- No. 126 Rueffler C, van Dooren TJM, Metz JAJ: *The Evolution of Resource Specialization Through Frequency-Dependent and Frequency-Independent Mechanisms*. IIASA Interim Report IR-06-073 (2006). *American Naturalist* 167:81-93 (2006).
- No. 127 Rueffler C, Egas M, Metz JAJ: *Evolutionary Predictions Should be Based on Individual Traits*. IIASA Interim Report IR-06-074 (2006). *American Naturalist* 168:148-162 (2006).
- No. 128 Kamo M, Sasaki A, Boots M: *The Role of Trade-Off Shapes in the Evolution of Virulence in Spatial Host-Parasite Interactions: An Approximate Analytical Approach*. IIASA Interim Report IR-06-075 (2006).
- No. 129 Boots M, Kamo M, Sasaki A: *The Implications of Spatial Structure Within Populations to the Evolution of Parasites*. IIASA Interim Report IR-06-078 (2006).
- No. 130 Andreasen V, Sasaki A: *Shaping the Phylogenetic Tree of Influenza by Cross-Immunity*. IIASA Interim Report IR-06-079 (2006).
- No. 131 Rueffler C, van Dooren TJM, Metz JAJ: *The Interplay Between Behavior and Morphology in the Evolutionary Dynamics of Resource Specialization*. IIASA Interim Report IR-06-082 (2006). *American Naturalist* 169:E34-E52 (2007).
- No. 132 Rueffler C, van Dooren TJM, Metz JAJ: *The Evolution of Simple Life-Histories: Steps Towards a Classification*. IIASA Interim Report IR-06-083 (2006).
- No. 133 Durinx M, Metz JAJ, Meszéna G: *Adaptive Dynamics for Physiologically Structured Population Models*. IIASA Interim Report IR-07-027 (2007).
- No. 134 Ito H, Dieckmann U: *A New Mechanism for Recurrent Adaptive Radiations*. IIASA Interim Report IR-07-048 (2007). *American Naturalist* 170:E96-E111 (2007).
- No. 135 Troost T, Kooi B, Dieckmann U: *Joint evolution of predator body size and prey-size preference*. IIASA Interim Report IR-07-050 (2007).

Issues of the IIASA Studies in Adaptive Dynamics series can be obtained at [www.iiasa.ac.at/Research/EEP/Series.html](http://www.iiasa.ac.at/Research/EEP/Series.html) or by writing to [eep@iiasa.ac.at](mailto:eep@iiasa.ac.at).

## Contents

Abstract.....	1
1. Introduction .....	2
2. Model description .....	3
2.1. Populaton dynamics.....	3
2.2. Scaling considerations .....	5
2.3. Incoming prey densities.....	7
2.4. Functional responses .....	7
2.5. Choice of units.....	10
3. Methods .....	11
3.1. Ecological analysis .....	11
3.2. Adaptive dynamics theory .....	12
3.3. Evolutionary analysis .....	14
4. Results .....	16
4.1. Ecological analysis .....	16
4.2. Evolutionary analysis .....	17
5. Discussion.....	18
5.1. True predators versus parasitic predators .....	18
5.2. Imperfect upper traingularity .....	19
5.3. Predator evolution under increased levels of ecological realism .....	21
5.4. Evolutionary effects of environmental factors .....	23
5.5. Evolutionary effects of feeding models.....	24
6. Conclusions .....	25
Acknowledgments .....	26
Appendix: Derivation of invasion fitness.....	27
References .....	32
Tables & Figures .....	37

# Joint evolution of predator body size and prey-size preference

Tineke A. Troost<sup>1</sup> and Bob W. Kooi

*Faculty of Earth and Life Sciences, Department of Theoretical Biology,  
Vrije Universiteit, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands*

and

Ulf Dieckmann

*Evolution and Ecology Program, International Institute for Applied Systems Analysis,  
Schlossplatz 1, 2361 Laxenburg, Austria*

## ABSTRACT

We studied the joint evolution of predator body size and prey-size preference based on dynamic energy budget theory. The predators' demography and their functional response are based on general eco-physiological principles involving the size of both predator and prey. While our model can account for qualitatively different predator types by adjusting parameter values, we mainly focused on 'true' predators that kill their prey. The resulting model explains various empirical observations, such as the triangular distribution of predator-prey size combinations, the island rule, and the difference in predator-prey size ratios between filter feeders and raptorial feeders. The model also reveals key factors for the evolution of predator-prey size ratios. Capture mechanisms turned out to have a large effect on this ratio, while prey-size availability and competition for resources only help explain variation in predator size, not variation in predator-prey size ratio. Predation among predators is identified as an important factor for deviations from the optimal predator-prey size ratio.

*Subject headings:* Body size; Prey-size preference; upper triangularity

---

<sup>1</sup>Corresponding author. Tel.: +31-20 598 7127; fax: +31-20 598 7123; e-mail: tineke@bio.vu.nl



## 1. Introduction

The range of body sizes encountered in nature is enormous. A bacterium with full physiological machinery has a volume of  $0.25 \times 10^{-18} \text{ m}^3$ , while a blue whale has a volume of up to  $135 \text{ m}^3$ . These body sizes are associated with the different scales in time and space in which organisms live, and reflect the differences in physiological processes and life histories. A wide range is also found in the prey-size preference of predators: consider, for example, whales feeding on plankton and hyena eating zebra. Like body size, prey-size preference is an important ecological property, as it determines which trophic links between predators and prey are established. Together, the body size and the prey-size preference of predators largely define the structure of a community. While the effects of body size on individuals and populations has been investigated from many angles (Peters 1983; Kooijman 1986; Yodzis and Innes 1992; Brown et al. 1993), general relationships between a predator's body size and its prey-size preference are more difficult to find.

Various mechanisms have been proposed that attempt to explain predator-prey size ratios and prey-size preferences. These include passive selection mechanisms such as prey visibility (Rincon and Loboncervia 1995; Svensson 1997) or gape limitation (Rincon and Loboncervia 1995; Forsman 1996; Mehner et al. 1998; Karpouzi and Stergiou 2003). Active selection mechanisms, on the other hand, underlie optimal foraging theory, which assumes that predators select prey sizes that provide the best energy returns. Several mechanisms based on active selection are discussed in Ellison and Gibson (1997), Manatunge and Aseada (1998), Rytkonen et al. (1998) Kristiansen et al. (2000), Tureson et al. (2002) and Husseman et al. (2003). However, since results vary both within and between predator-prey systems, and the found relationships are highly species-specific, it is difficult to extract general rules from them.

In recent years, several models have been developed that focus on general large-scale patterns of feeding links in food webs. Some of these models, such as the cascade model (Cohen and Newman 1985) and the niche model (Williams and Martinez 2000), are able to generate food webs that approximate many features observed in real food webs. However, these models are often descriptive and predator-prey pairs are assigned at random. Other models do have a more mechanistic basis and include physiological relations based on body size, but assume a fixed predator-prey size ratio (Loeuille and Loreau 2005). Aljetlawi et al. (2004) derived a functional response that accounts for both predator and prey size: the

derived relation was sufficiently flexible to be adjusted to many different specific predator-prey systems. This very flexibility, however, limits the scope for deriving general rules.

In this study we combine a process-based eco-physiological model with a functional response that depends on the size of both predator and prey. The model is based on dynamic energy budget (DEB) theory (Kooijman 2000, 2001), a versatile framework for modeling metabolic processes with physiological rules for uptake and use of material and energy. DEB theory does not specify all details of the size-dependence of the functional response. One of our aims here is to make the terms underlying this functional response explicit and, where necessary, include additional terms, while staying as close to DEB theory as possible.

We do not arbitrarily choose predator-prey size ratios, but instead we allow the predator size and its prey-size preference to evolve independently. The predators are supplied with prey that have a range of sizes. To keep the analysis feasible, we assume that the size distribution of prey is constant and does not evolve. The objective is to study which size combinations between predators and preys are feasible and to which predator-prey size ratios the considered population or community will eventually evolve. More specifically, we study how patterns of predator size and prey-size preference depend on various factors, given a fixed prey-size distribution; the examined factors include environmental parameters and ecological parameters, with the latter describing predation as well as competition. The model focuses on a generalized predator with two life stages, and therefore is not intended to replace more species-specific studies on size-selective prey choice. By retaining a general perspective, we hope that the results reported below will provide insights into the various factors determining predator-prey size ratios, and thereby will help understanding of predator-prey size patterns observed in nature.

## **2. Model description**

### **2.1. Population dynamics**

We consider a predator-prey model in which a population of predators feed on one or more populations of abiotic prey.

The predators are described by one state variable, their biomass density  $X_A$  (given by the total amount of structural biovolume per unit of system volume), and by two adaptive traits,

their adult length  $\ell_A$  and their preference for a prey length  $\ell_P$ . These two adaptive traits remain constant throughout an individual's life, but may change from parent to offspring through mutation. Prey populations are described by their biomass density  $X_i$ , and consist of organisms of length  $\ell_i$ , with  $i = 1, \dots, n$  where  $n$  is the number of prey populations. The prey populations are not interacting and are assumed to have a fixed size-structure. For example, we could consider algal populations grown in a first (illuminated) chemostat and fed into a second (dark) chemostat where they are consumed by rotifers (see Kooi and Kooijman 1999).

Our model for the predator is based on a model of a size-structured rotifer population (Kooi and Kooijman 1997, 1999), of which we use a simplified version that includes only two life stages for the predator, embryos and adults. Embryos do not feed, but grow by using the reserves they got from their mothers when eggs were produced. Adults, in contrast, do not grow but they do feed; the acquired energy is used for maintenance and egg production. Separating the functions of growth and feeding simplifies the model by reducing the number of equations. It also removes intraspecific body size scaling relations, but maintains inter-specific scaling relations. These include a size-dependent egg-production period  $a_A$  and a size-dependent developmental period  $a_b$  of the embryo. A continuous function for reproduction then allows the system to be expressed in terms of delay differential equations (DDEs). The dynamics of the system can then be described as follows,

$$\frac{d}{dt}X_i(t) = (X_{r,i} - X_i(t))D - I_i f_i(t) X_A(t), \quad (1a)$$

$$\frac{d}{dt}X_A(t) = R(t - a_b) \exp(-ha_b) X_A(t - a_b) - hX_A(t), \quad (1b)$$

where  $X_{r,i}$  is the incoming density of prey  $i$ ,  $f_i$  is the predator's functional response to prey  $i$  (to be further discussed in Section 2.4),  $I_i$  is the maximum volume-specific ingestion rate of prey  $i$  (which equals the inverse of the handling time  $[t_{h,i}]$  multiplied by the probability  $\rho_s$  that an attack is successful,  $I_i = \rho_s/[t_{h,i}]$ , where the square brackets indicate that the handling time is expressed on a volume-specific basis),  $D$  is the dilution rate of prey, and  $h$  is the predator's mortality rate. The delay in reproduction  $(t - a_b)$  is due to the predator's embryo development time  $a_b$ , which depends on how fast energy can be mobilized, as described by the specific energy conductance  $k_E$ ,  $a_b = 3/k_E$  (Kooi and Kooijman 1997). Embryos have the same mortality rate as adults, and the term  $\exp(-ha_b)$  accounts for the mortality of embryos during their development. The predator's reproduction rate is given by

$$R(t) = \frac{h}{\exp(ha_A(t)) - 1}, \quad (2)$$

(Kooi and Kooijman 1997), which depends on the mortality rate  $h$ . Generally, reproduction rates do not depend directly on adult mortality, but the expression above accounts for the death of eggs during the egg-production period caused by the mortality of (egg-producing) mothers. For small mortality rates, the reproduction rate equals the inverse of the egg-production period,  $R(t) = 1/a_A(t)$ .

An expression for  $a_A(t)$  was derived by Kooi and Kooijman (1997). Their expression is given by the ratio between the amount of energy needed per egg and the rate with which energy becomes available for reproduction. The latter depends on the scaled energy density  $e$  of the mother (i.e., on the volume-specific amount of energy  $[E]$  divided by the maximum energy content  $[E_{\max}]$ ) and on the specific energy conductance  $k_E$ . At equilibrium, the scaled energy density  $e$  of an adult equals its scaled functional response  $f$ , so that the amount of mobilized energy equals  $k_E f$ . From this mobilized energy, first the costs of maintenance have to be paid, calculated by multiplying the maintenance rate coefficient  $k_M$  (ratio of costs for maintenance per unit of time to costs for growth) with the energy investment ratio  $g$  (the proportion of the total amount of available energy that is used for growth). The scaled energy density required to produce an egg depends on the costs for the structural biomass of a newborn individual and the costs for growth and maintenance during the embryonic period,  $g^+ = g + \frac{3}{4}gk_M/k_E$  (Kooi and Kooijman 1997), as well as on the energy density of a newborn individual itself,  $\hat{e}$ . Based on these considerations, the egg-production period is obtained as

$$a_A(t) = \frac{g^+ + \hat{e}(t)}{k_E f(t) - k_M g}, \quad (3)$$

(Kooi and Kooijman 1997). For a more detailed explanation of the model, including derivations of  $a_b$ ,  $R$ ,  $a_A$ , and  $g^+$ , readers may want to consult the original work by Kooi and Kooijman (1997, 1999). All parameters and variables of the model are summarized in Table 1, with all default parameter values listed in Table 2.

## 2.2. Scaling considerations

Because this study considers adult length to be subject to evolution, some body-size scaling relations had to be included that were not taken into account in the original model (Kooi and Kooijman 1997, 1999), where body size was fixed. First, the energy investment ratio  $g$  was no longer assumed to be constant, but instead becomes dependent on body volume  $\ell_{\max}^3$ , following an expression central to DEB theory,  $g = v/(k_M \ell_{\max})$  (Kooijman 2000). Note

that the adult body size  $\ell_A$  of the predators is a fixed proportion  $\alpha$  of their maximum size,  $\ell_A = \alpha \ell_{\max}$ . This enables the model to cope with predators that quickly grow to adult size, without slowing down as would be expected from an asymptotic growth curve.

Second, the specific energy conductance  $k_E$  is equal to the energy conductance  $v$  divided by the size of the organism,  $k_E = v/\ell_A$ . The rationale behind this scaling relation is that energy is mobilized across membranes, which have a surface area proportional to that of the organism. As a result, the developmental period of the embryo becomes dependent on adult body size as well,  $a_b = 3\ell_A/v$ . Third, the mortality rate  $h$  was assumed to scale with length, such that larger organisms have a longer life span,  $h = D \ell_{\text{ref}}/\ell_A$ ; at the reference length  $\ell_{\text{ref}}$  mortality rate  $h$  is equal to dilution rate  $D$ . As such, the dilution rate serves as a measure for the harshness of the environment.

The scaled energy density of the eggs  $\hat{e}$  is assumed to depend on the scaled energy density  $e$  of the mother. In the original model (Kooi and Kooijman 1997, 1999), a mother would pass on to her eggs the precise amount of energy such that her offspring, after development and hatching, would have exactly the same energy density as herself. In this way the mother proportioned the amount of energy per egg, while ensuring that her offspring would have sufficient energy at the start of its life (right after hatching), at least as long as the environment did not change in the meanwhile. Also, it implied that once the system had reached its equilibrium (with respect to prey, predator, and energy densities), it would remain exactly at this equilibrium (Alver et al. 2006). Here, however, we study the evolution of prey size-preference, and the offspring may encounter or prefer different prey sizes than its mother. We therefore assume here that a mother takes into account these uncertainties. She does so by providing her offspring not just with the amount of energy to end up after hatching with the same energy density  $[E]$  she possesses, but with a larger energy density,  $[\hat{E}]$ , so that her offspring will always retain sufficient energy density after hatching, irrespective of the size of its prey. This is ensured by scaling the energy density of eggs, not against the mother's own maximum energy density  $[E_{\max}]$  (which depends on prey-size availability for her), but against the maximum possible energy density  $[E_{\max}]_{\text{ref}}$ . The corresponding scaled energy density  $\hat{e}$  is given by

$$\hat{e} = \frac{[\hat{E}]}{[E_{\max}]} = \frac{[\hat{E}]}{[E_{\max}]_{\text{ref}}} \frac{[E_{\max}]_{\text{ref}}}{[E_{\max}]} = \frac{[E_{\max}]_{\text{ref}}}{[E_{\max}]} e. \quad (4a)$$

If we again use  $e = f$ , this can be rewritten as

$$\hat{e} = \frac{[E_{\max}]_{\text{ref}}}{[E_{\max}]} e = \frac{[E_{\max}]_{\text{ref}}}{[E_{\max}]} f = \frac{[t_{\text{h}}]}{[t_{\text{h}}]_{\text{ref}}} f, \quad (4b)$$

where the last step follows from the fact that the maximum energy density is proportional to the maximum ingestion rate, while the maximum ingestion rate is the inverse of the handling time, so that  $[E_{\max}] \propto 1/[t_{\text{h}}]$ , (Kooijman 2000, p. 269).

### 2.3. Incoming prey densities

The model introduced above can be analyzed for one or more prey populations. In the latter case, the incoming prey densities  $X_{r,i}$  were assumed to vary gradually across prey populations, following a distribution with mean prey size  $\mu$ , (dimensionless) standard deviation  $\sigma$ , and maximum density  $X_{r,0}$ ,

$$X_{r,i} = X_{r,0} \frac{\delta}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2} \frac{\ln(\ell_i/\mu)^2}{\sigma^2}\right), \quad (5)$$

where  $\delta$  denotes the distance between the successive lengths of prey. For numerical purposes, this prey-size distribution was truncated at  $+3$  and at  $-3$  times the standard deviation  $\sigma$ , thus representing 98% of the total distribution. We found that a resolution of  $n = 50$  was sufficient to ensure that results were essentially unaffected by discretization of the prey-size distribution.

### 2.4. Functional responses

The sequence of capturing a prey consists of encounter, attack, and handling. These interactions between predator and prey are assumed to follow a Holling type-II functional response,

$$f = \sum_{i=1}^n f_i, \text{ with } f_i = \frac{X_i/K_i}{1 + \sum_{j=1}^n X_j/K_j} \text{ and } 1/K_i = \rho_{a,i} b_i [t_{\text{h},i}], \quad (6)$$

where  $K_i$  is the half-saturation constant of the functional response to prey  $i$ ,  $b_i$  is the volume-specific encounter rate of the predator with prey  $i$ ,  $\rho_{a,i}$  is the attack probability for prey  $i$ , and  $[t_{\text{h},i}]$  is the volume-specific time required for handling prey  $i$ . These terms and their

dependencies on the body sizes of both predator and prey,  $\ell_A$  and  $\ell_i$ , as well as on the prey-size preference of the predator,  $\ell_P$ , are discussed below. In line with DEB theory, we base these relationships on general scaling principles involving the lengths  $\ell$ , surface areas  $\ell^2$ , or volumes  $\ell^3$  of the considered organisms. As a result, the relations derived here are less detailed than the relations derived by, e.g., Aljetlawi et al. (2004); our assumption below of fixed scaling exponents also avoids problems with varying dimensions, and thus interpretations, of scaling coefficients.

**Encounter rate  $b$ .** The encounter rate  $b_i$  of a predator with a prey of size  $\ell_i$  arises from encounters within the predator’s search area. This search area is assumed to be proportional to the predator’s surface area,  $b \propto \ell_A^2$ , as is the case, for instance, for sessile filter feeders that orient their arms perpendicular to the current. For filter feeders that generate their own current, the encounter rate equals the filter rate. Their flapping or beating frequency is observed to be independent of their size (Kooijman 2000), such that the generated current is proportional to the surface area of their extremities, and thus again to their surface area. Other organisms may lay in ambush and capture prey that come within reach, i.e., within a distance that is proportional to the length of a leg or jaw or tongue, such that also here the encounter rate scales with surface area. Mobile organisms generally move with a speed proportional to their length: if the width of the path searched for food is proportional to length, this again leads to an encounter rate that scales with surface area. The encounter rate also scales with the surface area of the prey  $\ell_i^2$ , as the prey’s visibility or detectability is assumed to be proportional to the prey cross-sectional area or silhouette. In summary, we assume  $b_i \propto \ell_A^2 \ell_i^2$ . Because the population dynamics above were expressed on a per-volume basis,  $b_i$  is divided by the volumes of predator and prey, leading to the following relationship,

$$b_i = b_0 \frac{\ell_{\text{ref}}^2}{\ell_A \ell_i}, \quad (7)$$

where the lengths are measured relative to a reference length  $\ell_{\text{ref}}$ , so that the encounter rate coefficient  $b_0$ , which controls the absolute value of the encounter rate, has the same dimensions as  $b_i$ . Without any loss of generality, reference lengths were taken as equal for predator and prey.

**Attack probability  $\rho_a$ .** The predator prey-size preference  $\ell_P$  is assumed to evolve separately from the predator’s adult body size  $\ell_A$  and is not imposed by morphological constraints such

as limited gape size. Even though such structural limits may exist, we assume here that they are adjusted to the prey-size preference, rather than vice versa. The probability  $\rho_a$  with which a predator attacks a prey of size  $\ell_i$  is assumed to be log-normally distributed and depends on the prey-size preference  $\ell_p$  and (dimensionless) niche width  $\sigma_p$ ,

$$\rho_{a,i} = \exp\left(-\frac{1}{2} \frac{\ln(\ell_i/\ell_p)^2}{\sigma_p^2}\right). \quad (8)$$

On encounter, a prey exactly of the preferred size  $\ell_p$  will thus be attacked with certainty.

**Handling time  $t_h$ .** In general, the time required for handling each prey item comprises the time needed for capture and ingestion.

Ingestion is the process by which the prey is physically taken up into the body of the predator, passing through, for instance, its outer membrane or its gut wall. First of all, ingestion time  $t_g$  is assumed to be proportional to the amount of prey biomass that has to be ingested, and thus, for one prey individual, proportional to the prey volume,  $t_{g,i} \propto \ell_i^3$ .

In addition, for *intraspecific* comparisons, DEB theory assumes the ingestion time to be inversely proportional to the surface area through which the intake occurs, and this surface area is assumed to scale with the total surface area  $\ell_A^2$  of the predator. For small individuals, which have a favorable ratio between surface area and volume, the ingestion time thus is small, while for larger individuals, it is large. In this study, however, we assume all adult individuals of a population to have the same size,  $\ell_A$ . For *interspecific* comparisons, DEB theory assumes ingestion rates to be proportional to maximum length,  $\ell_{\max}$ , which implies that  $t_g \propto \ell_{\max}^{-1}$ . Such a scaling may, for instance, be related to gut capacity (body plan) or diet composition of the predator.

Capture time is assumed to depend on the relative sizes of predator and prey. Larger prey require a longer capture time because they may be better protected, resist more strongly, or have to be cut into chunks before being ingested. Specifically, we assume that the capture time increases faster with prey size than does the corresponding yield, which implies that it is proportional to size with an exponent larger than 3; as a default, here, we assume an exponent of 4,  $t_c \propto (\ell_i/\ell_A)^4$ .

The total handling time  $t_h$  equals the mean length of the handling process, consisting of



capture and ingestion,

$$\begin{aligned} t_{h,i} &= t_{c,i} + \rho_s t_{g,i} \\ &= t_{c,0} \left(\frac{\ell_i}{\ell_A}\right)^4 + \rho_s \frac{t_{g,0}}{\ell_{\max}} \frac{\ell_i^3}{\ell_A^2}, \end{aligned} \quad (9)$$

where  $t_{g,0}$  and  $t_{c,0}$  are the ingestion and capture coefficients, and  $\rho_s$  is the fraction of attacked prey that is actually captured; only this fraction has to be ingested. As a default, all attacks are assumed to be successful,  $\rho_s = 1$ ; the effects of reduced capture efficiencies are studied in Section 5.5.

Because adult size increases with maximum size, and since all adult organisms are assumed to possess adult size,  $\ell_{\max}$  can be substituted with  $\ell_A/\alpha$ . The time  $t_{h,i}$  that a predator needs for handling an individual of prey  $i$  can be converted into the volume-specific handling time  $[t_{h,i}]$ , which measures the time that a volume-unit of predator needs for handling a volume-unit of prey  $i$ , through multiplication with  $(\ell_A/\ell_i)^3$ ,

$$[t_{h,i}] = [t_{c,0}] \frac{\ell_i}{\ell_A} + \rho_s \alpha [t_{g,0}]. \quad (10)$$

The total handling time  $[t_h]$  given the actual prey-size availability is the sum of prey-size specific handling times  $[t_{h,i}]$  weighted with the fraction  $\theta_i$  of all attacks that are directed at prey  $i$ ,

$$[t_h] = \sum_{i=1}^n \theta_i [t_{h,i}], \quad \text{with } \theta_i = \frac{\rho_{a,i} b_i X_i}{\sum_{j=1}^n \rho_{a,j} b_j X_j}. \quad (11)$$

Finally,  $[t_h]_{\text{ref}}$  in Equation (4b) is the absolute minimum, or reference, handling time, which equals  $[t_{h,i}]$  at infinitely small prey-sizes,  $[t_h]_{\text{ref}} = [t_{h,i}]|_{\ell_i=0} = \rho_s \alpha t_{g,0}$ , and thus only depends on predator size.

## 2.5. Choice of units

The model presented above was scaled by maintenance rate  $k_M$ , energy conductance  $v$ , and incoming prey density coefficient  $X_{r,0}$ . Scaling renders the outcomes independent of these parameters. The unit of time,  $T$ , is chosen as  $k_M^{-1}$ , the unit of predator and prey length,  $L$ , is chosen as  $v/k_M$ , and the unit of reactor length,  $l$ , is chosen as  $\sqrt[3]{X_{r,0}} k_M/v$ ; the latter unit, however, only features in the dimensions of biomass-volume densities,  $L^3 l^{-3}$ , which are made dimensionless simply through division by  $X_{r,0}$ .

The remaining variables and parameters, which then become dimensionless, are denoted by a tilde: for instance, the predator size  $\ell_A$  (dim:  $L$ ) was divided by  $v$  (dim:  $LT^{-1}$ ) and multiplied by  $k_M$  (dim:  $T^{-1}$ ) so that the scaled length  $\tilde{\ell}_A$  is dimensionless. The scaled predator and prey densities are indicated by  $x$  instead of  $X$ , e.g.,  $x_A = X_A/X_{r,0}$ , and the scaled time  $t$  is indicated by  $\tau$ . The default values of the scaled parameters are shown in Table 2. The scaled model can thus be written as follows,

$$\frac{dx_i}{d\tau} = (x_{r,i} - x_i)\tilde{D} - \tilde{I}_i f_i x_A(\tau), \quad (12a)$$

$$\frac{dx_A}{d\tau} = \tilde{R}(\tau - \tilde{a}_b) \exp(-\tilde{h}\tilde{a}_b) x_A(\tau - \tilde{a}_b) - \tilde{h}x_A(\tau). \quad (12b)$$

The scaled reproduction rate  $\tilde{R}$  is given by

$$\tilde{R}(\tau) = \frac{\tilde{h}}{\exp(\tilde{h}(g^+ + \hat{e}(\tau))(f(\tau)/\tilde{\ell}_A - g)^{-1}) - 1}, \quad (13)$$

where  $f$  is the functional response, as given in Equation (6), and  $\hat{e}$  is the scaled energy density of an egg, as given in Equations (4). Furthermore,  $\tilde{D}$  is the scaled dilution rate,  $\tilde{h} = \tilde{D}\tilde{\ell}_{\text{ref}}/\tilde{\ell}_A$  is the mortality rate,  $\tilde{a}_b = 3\tilde{\ell}_A$  is the scaled egg development rate,  $g$  is the energy investment ratio,  $g = \alpha/\tilde{\ell}_A$ , and  $g^+ = g + \frac{3}{4}\alpha$  is the difference in reserve density between the beginning and end of egg development. Note that  $f$ ,  $g$ , and  $\hat{e}$  already were dimensionless variables before, and are therefore not affected by any choice of units.

### 3. Methods

#### 3.1. Ecological analysis

The coexistence set is the region in the trait space of the predator's body size  $\tilde{\ell}_A$  and its prey-size preference  $\tilde{\ell}_p$  in which the predator and prey populations can coexist, i.e., where  $x_i^* > 0$  for  $i = 1, \dots, n$  and  $x_A^* > 0$ . Here and below, a superscripted asterisk indicates a population equilibrium, e.g., the scaled reproduction rate at equilibrium is denoted by  $\tilde{R}^*$ . At each point of this trait space there also exists a boundary equilibrium,  $x_A^* = 0$  and  $x_i^* = x_{r,i}$ , which is unstable for trait combinations within the coexistence set and stable for those outside. In other words, the boundary of the coexistence set is formed by trait combinations for which the boundary equilibrium changes stability. Consequently, only within the coexistence set there is a positive equilibrium of the prey-predator system. The resulting figure (Figure 1) showing the coexistence set is explained in more detail in Section 4.1.

We restrict the discussion of the coexistence set to the case in which a single prey population is supplied to the system. This enables us to check whether a predator can coexist with prey of a specific size, without this being influenced by the precise choice of niche width or prey-size distribution. Accordingly, we assume that the prey-size preference of the predator matches exactly the one available prey size,  $\tilde{\ell}_P = \tilde{\ell}_1$ . This cuts short the evolution of prey-size preference, which will evolve to the size of the available prey anyway (as this is the only one available). The resulting coexistence set will thus show which predators can live on which prey. More precisely, the set shows whether a predator of certain size can coexist with a prey of a certain size when these prey are of the predator’s preferred size.

An equilibrium point on the boundary of the coexistence set is given by  $(\tilde{\ell}_A, \tilde{\ell}_P = \tilde{\ell}_1)$  for which  $x_1^* = x_{r,1}$ ,  $x_A^* = 0$ , and  $\tilde{R}^* \exp(-\tilde{h}\tilde{a}_b) = \tilde{h}$ , where  $\tilde{R}^*$  is the equilibrium value of  $\tilde{R}$  in Equation (13). The remaining points  $(\tilde{\ell}_A, \tilde{\ell}_P = \tilde{\ell}_1)$  on the boundary of the coexistence set were then determined by numerically continuing this condition using standard continuation software.

### 3.2. Adaptive dynamics theory

For the evolutionary analysis of our model we utilized adaptive dynamics theory, a general framework that helps investigate phenotypic evolution under frequency-dependent selection (Dieckmann and Law 1996; Metz et al. 1996; Dieckmann 1997; Geritz et al. 1997). This approach assumes a time scale separation between the ecological and evolutionary dynamics, so that mutations in adaptive traits occur sufficiently rarely for the considered resident population always to be close to its population dynamical equilibrium when probed by a mutant. Mutants with a positive invasion fitness may replace the resident population. A series of such replacements leads to phenotypic change of the population. The directions and endpoints of phenotypic change depend on the selection gradient and are calculated by means of the so-called canonical equation of adaptive dynamics (Dieckmann and Law 1996). Below we specify, in turn, these general notions for the model analyzed in this study.

**Invasion fitness.** The invasion fitness of a mutant is defined by its long-term per capita growth rate  $r(\tilde{\ell}_m, E_r(\tilde{\ell}_r))$  while being rare in the environment  $E_r$  set by the resident population at its ecological equilibrium. Here,  $\tilde{\ell}$  is the vector of the predator’s adaptive traits

$\tilde{\ell} = (\tilde{\ell}_A, \tilde{\ell}_P)$  and the subscripts ‘r’ and ‘m’ indicate resident and mutant trait values, respectively. To calculate the invasion fitness of the mutant we extend Equations (12) by including the dynamics of the mutant predator,

$$\frac{dx_{A,m}}{d\tau} = \tilde{R}_m(\tau - \tilde{a}_{b,m}) \exp(-\tilde{h}_m \tilde{a}_{b,m} x_{A,m}(\tau - \tilde{a}_b) - \tilde{h}_m x_{A,m}(\tau)). \quad (14)$$

Introducing a mutant in the system also requires a feeding term to be added to Equation (12a), as shown in Equation (21a).

As explained in detail in the appendix (Equation 31), the invasion fitness of the mutant is thus given by

$$s(\tilde{\ell}_m, \tilde{\ell}_r) = \tilde{R}_m^* \exp(-\tilde{h}_m \tilde{a}_{b,m}) - \tilde{h}_m, \quad (15)$$

where  $\tilde{R}_m^*$  is the mutant’s reproduction rate at the system’s equilibrium,

$$\tilde{R}_m^* = \frac{\tilde{h}_m}{\exp(\tilde{h}_m(g_m^+ + \hat{e}_m)/(f_m/\tilde{\ell}_{A,m} - g_m)) - 1}. \quad (16)$$

Here the functional response  $f_m$  of the mutant depends on the adaptive traits of both mutant and resident, because the resident predator sets the environment  $E_r$  and thus determines the equilibrium prey density in the system.

**Selection gradient.** The expected direction of phenotypic change is proportional to the selection gradient, i.e., to the derivative of invasion fitness with respect to the adaptive traits of the mutant, evaluated at the trait values of the resident. For a monomorphic resident population, this selection gradient is denoted by

$$\nabla_m s(\tilde{\ell}_m, \tilde{\ell}_r) = \left( \frac{\partial}{\partial \tilde{\ell}_{A,m}} s(\tilde{\ell}_m, \tilde{\ell}_r), \frac{\partial}{\partial \tilde{\ell}_{P,m}} s(\tilde{\ell}_m, \tilde{\ell}_r) \right) \Big|_{\tilde{\ell}_m = \tilde{\ell}_r}. \quad (17)$$

**Canonical equation.** A deterministic approximation of the stochastic evolutionary trajectories of body size and prey-size preference, jointly driven by mutation and selection, is provided by the canonical equation of adaptive dynamics (Dieckmann and Law 1996), which for our system is given by

$$\frac{d\tilde{\ell}_r}{dt} = \rho(\tilde{\ell}_r) \frac{x_{A,r}^*}{\tilde{\ell}_{A,r}^3} \nabla_m s(\tilde{\ell}_m, \tilde{\ell}_r). \quad (18)$$

Here  $\rho$  is a compound parameter consisting of the product of the  $2 \times 2$  variance-covariance matrix of the multivariate mutation distribution (Dieckmann and Law 1996), the factor 1/2,

the mutation probability, and the coefficient of variation of clutch sizes. As mutations in the two predator traits are assumed to be independent, the variance-covariance matrix of the mutation distribution is a diagonal matrix. The value of  $\rho$  is irrelevant for this study as we are only interested in evolutionary equilibria, and not in the timing of the trajectories leading towards them.

**Evolutionary outcomes.** Eventually, the population will reach a combination of trait values  $\tilde{\ell}_r$  at which the selection gradient vanishes,

$$\nabla_{\mathbf{m}} s(\tilde{\ell}_m, \tilde{\ell}_r) = 0. \quad (19)$$

Such an evolutionary equilibrium may be either stable or unstable according to Equation (18). An evolutionary equilibrium may also be situated at a fitness maximum, a fitness minimum, or a fitness saddle according to Equation (15). In the latter two cases, the evolutionary equilibrium is not locally evolutionarily stable, so that the resident population may split up and evolve into two or more subpopulations through a process known as evolutionary branching (Metz et al. 1992, 1996; Geritz et al. 1997, 1998).

### 3.3. Evolutionary analysis

**Single-trait evolution.** As a preparatory step in the evolutionary analysis of our model, we focus on the evolution of the predator’s body size. For this purpose we assumed, like in the ecological analysis, that only a single prey population exists and that the predator’s prey-size preference always matches this prey size,  $\tilde{\ell}_p = \tilde{\ell}_1$ . In this case, the evolutionary dynamics are reduced to the single trait  $\tilde{\ell}_A$ . The evolutionary outcome of  $\tilde{\ell}_A$  represents the body size towards which a predator will evolve when feeding on prey of a certain size. This evolutionary body size was found numerically by integrating the dynamics of  $\tilde{\ell}_A$  according to the canonical equation of adaptive dynamics, Equation (18), while keeping  $\tilde{\ell}_p$  and  $\tilde{\ell}_1$  fixed, until an evolutionary equilibrium was reached. This evolutionary equilibrium was then determined for a range of prey sizes (and thus prey-size preferences) within the coexistence set.

**Two-trait evolution.** The full evolutionary dynamics were studied by allowing the two adaptive traits of the predator to evolve jointly. In this case, a range of prey sizes was assumed

to be available to the predator according to Equation (5). The evolutionary equilibrium was again found numerically, by integrating Equation (18).

**Evolutionary branching.** To study the evolutionary process after an evolutionary equilibrium had been reached, an extended numerical analysis was carried out. This analysis consisted of first integrating Equation (18) until reaching an evolutionary equilibrium. If this equilibrium was evolutionarily unstable, i.e., if it corresponded to a fitness minimum or fitness saddle, the original predator population was equally split into two predator populations and the two corresponding canonical equations were considered further. The trait values of the two predator populations were chosen to deviate slightly from that of their ancestor in the two (opposite) directions of highest fitness increase around the ancestral combination of trait values. The two canonical equations were integrated, and new predator populations were added analogously if applicable, until a locally evolutionarily stable evolutionary equilibrium was reached, corresponding to a fitness maximum in all predator populations. Due to the deterministic nature of the adaptive dynamics, more than one predator population may branch at the same time.

**Mutual predation.** Finally, to explore the effects of predation among predators, the functional response  $f$  was calculated as the sum of partial functional responses  $f_i$ , where  $i$  now consisted of all prey populations ( $i = 1, \dots, n$ ) as well as of all predator populations ( $i = n + 1, \dots, p$ ),

$$f = \sum_{i=1}^{n+p} f_i. \quad (20)$$

**Stochastic evolution.** As a further robustness test, we used a stochastic simulation process instead of the deterministic dynamics in Equation (18). Underlying equations were adjusted for multiple prey populations as discussed at the end of the appendix. We repeatedly integrated the ecological dynamics of the system for  $10^4$  time steps, followed by the addition of a new mutant predator population to the system. The trait values of the mutant were drawn at random from a normal distribution around the trait values of its ancestor with a standard deviation of  $10^{-3}$ . The initial biomass of the mutant population was set to a very small value,  $x_{A,m} = 10^{-20}$ . This value was also used as the cutoff biomass density below which a population was assumed to go extinct. In the case of extinction, the affected population was

removed from the system.

## 4. Results

### 4.1. Ecological analysis

We start by studying which predator-prey size combinations can coexist. As explained above, we restrict the analysis of the coexistence set to the case in which a single prey population is supplied to the system. For this analysis, the predator’s prey-size preference equals the single available prey size assumed to be available,  $\tilde{\ell}_p = \tilde{\ell}_1$ . The resultant coexistence set is shown in Figure 1. This figure can be interpreted in two ways: vertically, as the feasible range of predator body sizes for a given prey size (illustrated by arrow 1), and horizontally, as the feasible range of prey-size preferences for a given predator body size (illustrated by arrow 2).

We separately determined the coexistence set for two different functional responses. First, only the basic handling processes of encountering and ingesting prey were assumed to play a role in the functional response of the predator ( $[\tilde{t}_{c,0}] = 0$ , for other parameter values see Table 2). In this case, Figure 1 shows that the maximum feasible predator body size is inversely related to the maximum feasible prey size (dashed line). Second, the model was extended by including a capture time that depends on the predator-prey size ratio. Now, large predator-prey size ratios are no longer feasible, and the boundary of the coexistence set becomes curvilinear (continuous curve).

Figure 2 shows a set of empirically observed combinations of predator-prey sizes that were presented by Cohen et al. (1993), together with the coexistence set of our model based on a size-ratio-dependent capture time (continuous curve). The empirical data set consists of 478 size combinations from 30 food webs. In the doubly logarithmic plot, these are distributed over a triangular area that is bounded above by a maximum predator size, bounded below by the equality of predator and prey sizes, and bounded on the left by the minimum prey size. The coexistence sets in Figures 1 and 2 (continuous curves) are identical, but for Figure 2 the length variables are translated back from dimensionless variables into lengths expressed in centimeters. For the two relevant scaling parameters,  $k_M$  and  $v$ , reasonable values were chosen that lie well within the range of empirically observed values ( $k_M = 1.44 \text{ d}^{-1}$ ,  $v = 0.3 \text{ cm d}^{-1}$ ; Kooijman 2000); the dilution rate was adjusted ( $\tilde{D} = 0.05$ ) so as to obtain a

slightly better fit for the upper boundary of the coexistence set.

## 4.2. Evolutionary analysis

After having established which combinations of a predator’s body size and its prey-size preference are ecologically feasible, we also studied the evolutionary dynamics of these adaptive traits. Figure 3 again shows the coexistence set (continuous curve) and the diagonal along which predator size and prey-size preference are equal (dotted line). The dashed line shows the body size to which the predator will evolve when feeding on a prey of a given size. In other words, it shows how the evolutionary equilibrium depends on prey size. This line results from single-trait evolution in  $\ell_A$ , and applies when only one prey size is available and  $\tilde{\ell}_p = \tilde{\ell}_1$ . The figure shows that the evolved predator size is positively correlated with prey size, and that the slope of the correlation line is equal to unity.

When, instead of one prey size, a range of prey sizes is available simultaneously to the predator, as described in Section 2.3, and both traits are allowed to evolve jointly, the predator population evolves to an evolutionary equilibrium within the coexistence set, which in Figure 3 is denoted by an asterisk.

However, after this evolutionary equilibrium is reached, evolution continues. Since the evolutionary equilibrium does not correspond to an evolutionarily stable fitness maximum, the originally monomorphic predator population splits up into two populations and thus becomes dimorphic. This process of evolutionary branching is repeated several times, such that the predator population cascades into a range of populations with different trait combinations, until a locally evolutionarily stable predator community is eventually reached. In Figure 3 the trait combinations realized in this evolved community are shown by filled circles.

Inclusion of predation among predators also leads to sequential evolutionary branching. The trait combinations resulting under stochastic evolution after 5000 mutations are shown in as open circles in Figure 3; at this point in time the system is close to a locally evolutionarily stable equilibrium. The slightly irregular spacing of the realized trait combinations reflects the stochastic nature of the evolutionary process.

Figure 4 shows how the predator’s body size and prey-size preference at the initial evolutionary equilibrium (i.e., before the first evolutionary branching) are affected by the avail-



ability of prey sizes. Specifically, the three panels show how the predator’s adaptive traits vary with three features of the prey: the mean  $\tilde{\mu}$  and standard deviation  $\sigma$  of the prey-size distribution, and the prey’s dilution rate  $\tilde{D}$ . Analogously, Figure 5 shows the variation of the predator’s adaptive traits with two features of the predator: its niche width  $\sigma_p$  and its probability  $\rho_s$  of successfully capturing an attacked prey.

## 5. Discussion

In the first two subsections below we discuss the results of our ecological analysis, followed by three subsections of discussion on the results of our evolutionary analysis.

### 5.1. True predators versus parasitic predators

When taking into account only the basic handling processes of encountering and ingesting of prey, small predator-prey size ratios are feasible (Figure 1, dashed line). Clearly, this does not agree with the distribution of empirically observed predator-prey sizes shown in Figure 2. However, small size ratios are typically found in parasite-host systems (Memmott et al. 2000), which were not included in the empirical dataset of Cohen et al. (1993). Parasites are organisms that obtain their nutrients from one or very few host individuals, causing harm but no (immediate) death. True predators, in contrast, continuously require new prey individuals, which are killed at attack or quickly thereafter. Because parasites do not have to overpower their prey, capture times may be neglected. Under these circumstances, our model predicts that small predator-prey size ratios are feasible, in qualitative agreement with empirical data.

The transition between parasites and true predators, however, is gradual. This is illustrated by the typical classification of a bird-egg eating snake as a predator, while the sea-cucumber-egg eating pearlfish is classified as a parasite. Examples from the wide range of parasitic relationships are discussed by Combes (2001). Whatever classification rules are defined, many exceptions can be found, pointing to the fact that these boundaries are essentially artificial. DEB theory assumes that predators and parasites are basically of the same kind, and only differ physiologically. The resulting differences in their parameter values, however, may lead to considerable, even qualitative, differences in the feasibility of predator-prey size com-

binations. In the results of our model, this is reflected by the qualitative change in the shape of the coexistence set when capture times are considered (Figure 1, continuous curve). In this case, the coexistence set is shrunk and it is no longer feasible for small predators to feed on large prey.

Hence, by adjusting capture times in our model (e.g., by varying the capture time coefficient), we can account for both parasites and true predators. Similarly, by adjusting other parameter values, our model may also be expected to account for other types of predators, such as grazers or parasitoids. As a default, however, we considered a capture time coefficient that is relatively large, implying that the model mainly corresponds to true predators.

## 5.2. Imperfect upper triangularity

When including in our model a capture time that depends on the predator-prey size ratio, the feasible set becomes triangularly shaped (Figure 1, continuous curve), which matches the empirical distribution of observed predator-prey size combinations presented by Cohen et al. (1993) (Figure 2). This so-called ‘upper triangularity’ is often found in real food webs (Warren and Lawton 1987; Cohen et al. 1993, 2003). The term stems from considering a food web’s matrix of trophic interaction coefficients, in which species are arranged in hierarchical order, such that all of the non-zero matrix elements lie above the main diagonal. In the present study, the emergence of upper triangularity implies that larger predators can feed on a wider range of prey sizes and that for smaller prey sizes, the feasible range of predator sizes is wider. It also implies that a given species essentially does not eat other species that are larger than itself, which suggests a body-size-based hierarchy. Body size has been suggested previously to provide a mechanistic interpretation for the hierarchy assumption in the cascade model (Cohen and Newman 1985), both by Warren and Lawton (1987) and by Cohen (1989). However, in our analysis we did not postulate a size hierarchy as such: instead, this hierarchy naturally emerges from the scaling relations and size-dependent functional response suggested by DEB theory, and in particular from the considered proportionality of capture time to predator-prey size ratio.

The value of the capture time coefficient  $[\tilde{t}_{c,0}]$  considerably affects the shape of the coexistence set. Yet, when plotted on a doubly logarithmic scale, different values of  $[\tilde{t}_{c,0}]$  all result in a lower boundary of the coexistence set given by a straight line with slope one, cor-

responding to a fixed predator-prey size ratio. Although these lines have different intercepts, they lie rather close to each other and to the main diagonal for a relatively large range of values for  $[\tilde{t}_{c,0}]$ , especially when large predator and prey size ranges are considered. This finding would explain why, across many natural systems, the distribution of body size combinations involved in predator-prey links seems to be essentially the same.

Although the predicted boundaries of the coexistence set fit the empirical data reasonably, the fit is not perfect. For example, part of the predicted curvilinear upper boundary of the coexistence set, corresponding to combinations of small prey sizes with large predator sizes, is not observed in the considered empirical dataset. Instead, the upper boundary in the empirical dataset may be described simply by the body size of predators maxing out at about 150 cm to 200 cm. In the model, this curvilinear upper boundary is mainly determined by the encounter rate between predator and prey being proportional to the prey's surface area. Apparently, in natural systems, this is not realistic for large predators in combination with small prey. Probably, at these size ratios, the prey is not detected by vision, and the detectability may not be proportional to a prey's silhouette. This implies that the model's fit in this range of size combinations could be improved by including additional mechanisms. However, we chose to keep our model simple and to stay in line with DEB theory by including as few additional assumptions as possible.

An interesting property of the model is that the predicted lower boundary of the predicted coexistence set (Figure 2, continuous curve) does not coincide with the diagonal along which predator and prey sizes are equal (dotted line), but instead lies below it (as discussed above, the exact location of this lower boundary depends on parameter values, and especially on the capture time coefficient  $[\tilde{t}_{c,0}]$ ). The coexistence set thus extends to predators feeding on prey individuals that are larger than themselves.

Cohen et al. (1993) found that, in their dataset, approximately 10% of all predators fed on larger prey. Empirical studies have demonstrated this effect also for other natural food webs. Because of these consistent observations, the simple cascade model (Cohen and Newman 1985) has been extended, resulting in the more general niche model (Williams and Martinez 2000), which is viewed as providing better matches with empirical food web data (Warren and Lawton 1987; Neubert et al. 2000; Cohen et al. 2003). The proposed explanations are all based on the assumption that a certain hierarchy exists, but that the measures or variables used to characterize it may be imperfect. In contrast, the size-ratio-

dependent capture time assumed in our model provides a mechanism that naturally explains a body-size-based hierarchy while also allowing for ‘exceptional’ predator-prey links. This result suggests that not the measures or the variables, but rather the hierarchy itself is imperfect.

### 5.3. Predator evolution under increased levels of ecological realism

Our approach allows us to study and disentangle the evolutionary effects caused by the successive incorporation into our model of

increased levels of ecological realism. Five such steps have been taken. First, we started out from a system in which a single predator adapts to a single prey. Second, we investigated the joint evolution of the body size and prey-size preference of a single predator confronted with a range of prey sizes. Third, we considered the adaptive radiation of predator types caused by resource competition. Fourth, we included trophic interactions among predators to examine their effects on the outcomes of predator radiation. Fifth, we included evolutionary stochasticity in our model, to corroborate the robustness of our deterministic predictions.

Figure 3 shows that when a single predator adapts to a single prey, predator body size is positively correlated with prey body size, with a slope equal to 1. This implies that the predators evolve to a fixed predator-prey size ratio that is constant across predator sizes. A positive correlation between body sizes of predator and prey is indeed found in vertebrates (Gittleman 1985; Vezina 1985) and invertebrates (Warren and Lawton 1987), as well as in planktonic predators (Hansen et al. 1994). Even though these studies underscore that a general and fixed size ratio does not exist, they do find a constant size ratio within each trophic or taxonomic group.

When, instead of one prey size, a range of prey sizes is available simultaneously to the predator, and the body size and prey-size preference of a single predator evolve jointly, the size ratio at the resultant evolutionary equilibrium (asterisk in Figure 3) is slightly different from that resulting from single-trait evolution (dashed line in Figure 3). This is because now a range of prey sizes is available, so that the predator’s niche width comes to play a role. The effects of varying this niche width are discussed in detail in Section 5.5.

Were the range of prey sizes not bounded, the predators would evolve towards ever smaller body sizes. This is inherent to their physiology, which favors small sizes over large

ones: large organisms have relatively more energy reserves, and therefore a relatively longer egg-production period, which negatively affects their reproduction rate. Also, smaller organisms have a relatively large surface area, which is favorable with respect to the encounter and ingestion rates which both scale with surface area. Apparently, many physiological mechanisms favor a smaller size. Two factors that, by contrast, may induce evolution towards larger body sizes are heat loss and environmental variability. The tendency of organisms living at high latitudes to evolve to large body sizes has become known as Bergmann's rule (Bergmann 1847; Mayr 1956, 1963), and is often ascribed to the favorable effects of lower surface-area-to-volume ratios on heat loss. Environmental variability brings about periods of elevated starvation danger against which a large body size protects, as larger organisms possess larger energy reserves. These two factors, however, were not considered in the present study.

Figure 3 (filled circles) shows the trait combinations of the predator populations that will eventually result from deterministic evolution when adaptive radiations are considered. The mechanism underlying the evolutionary branching events is competition for resources, which leads to disruptive selection. The evolutionary branching process affects both adaptive traits: under the force of disruptive selection, some populations evolve towards smaller body sizes *and* smaller prey-size preferences, while others evolve to larger body sizes *and* larger prey-size preferences. When they are isolated, each of the populations (filled circles) will again evolve towards the first evolutionary equilibrium (asterisk). The latter may correspond to evolutionary processes on some islands, where small mammal species have been observed to evolve to a larger size and larger species to a smaller size. Such a tendency has become known as the 'island rule' (Van Valen 1973), and can thus be understood by the evolutionary dynamics in our model. Figure 3 also shows that all resulting populations retain the same predator-prey size ratio. From this it can be concluded that competition for resources may lead to the differentiation of predator body sizes and prey-size preferences, but not to a differentiation of predator-prey size ratios.

In determining these evolutionary outcomes, direct interactions among predators, either through predation or through interference competition, were not taken into account. Therefore, these outcomes clearly correspond to idealized conditions. Real organisms may only conform to the resultant predictions in situations in which competition and predation among predators are naturally absent.

Predation among predators or direct (interference) competition, on the other hand, may

give an additional advantage to large body sizes: larger organisms can be preyed upon by a smaller range of predators and are thus less vulnerable to predation (as follows from the triangular distribution of empirical predator-prey combinations), and they may also have an advantage in the direct competition for food or territory. As such, these processes may be expected to cause organisms to depart from the predator-prey size ratios predicted above.

Figure 3 (open circles) shows that predation among predators does indeed lead to much larger predator-prey size ratios than would be expected on the basis of resource competition alone. Predation among predators may thus indeed be an important factor for explaining the large variation of predator-prey size ratios found in nature. Direct (interference) competition is expected to have a similar effect as predation among predators. Both factors help explain Cope’s rule (Cope 1896; Benton 2002), which states that natural selection will tend to produce large-bodied species.

Predictions of deterministic and stochastic renderings of the evolutionary dynamics in our model agree almost completely, even though the stochastic dynamics expectedly induce a slight amount of jitter in the evolved predator communities (open circles in Figure 3).

#### 5.4. Evolutionary effects of environmental factors

Figures 4a and 4b show how the outcomes of evolution in predator body size and prey-size preference are affected by the availability of prey sizes. An increase in the mean  $\bar{\mu}$  of the prey-size distribution causes both traits to increase (Figure 4a), while the response to variations in the standard deviation  $\sigma$  of the prey-size distribution turns out to be hump-shaped (Figure 4b). Although the evolved values of the scaled predator body size  $\tilde{\ell}_A$  and prey-size preference  $\tilde{\ell}_P$  change, their ratio remains essentially constant across a large range of the studied parameter values. Changes in the prey-size distribution, expressed in terms of  $\bar{\mu}$  and  $\sigma$ , may thus induce shifts in predator body sizes and prey-size preferences, but cannot explain the variation observed in predator-prey size ratios.

In contrast, an increase in dilution rate does change the evolved size ratio by making it larger. The evolved body size of predators is affected by the dilution rate through changes in food abundance: smaller dilution rates reduce both the rate at which new prey enter the system and the mortality of predators, thus intensifying conspecific competition for resources. The resulting decrease in evolved predator body size may correspond to the tendency to

dwarfism on islands, which also has been related to limited food resources (Case 1978).

### 5.5. Evolutionary effects of feeding modes

Ecological factors, such as the predator's feeding mode, may also affect the evolutionary outcomes of predator body size and prey-size preference. In particular, a difference between the predator-prey size ratio of filter feeders and raptorial feeders is seen across taxonomic groups. Hansen et al. (1994) found that the optimal size ratio of filter feeders is larger than that of raptorial feeders. They also found that filter feeders generally feed on a larger range of prey sizes than raptorial feeders. To examine whether the wider prey range can explain the differences in size ratios, we studied the evolutionary effects of varying the niche width  $\sigma_P$  of the predator. Figure 5a shows that the predator-prey size ratio first increases with niche width and then stabilizes. As the niche width goes to zero, the predator evolves towards a preference for the smallest prey size that is still available. In this case, the predator-prey size ratio becomes equal to the size ratio that was predicted from single-trait evolution; this is expected, as in that analysis the predator was assumed to feed on one prey size only, which corresponds to vanishing niche width.

Although raptorial feeders may be more size-selective, it is conceivable that they are also more efficient predators, with a larger fraction of their attacks being successful. Therefore, we also studied the evolutionary effects of varying the capture efficiency  $\rho_s$ . Figure 5b shows that when a predator is less successful, its body size will become larger, while its prey-size preference will become smaller. Successful predators will thus evolve towards smaller predator-prey size ratios. Combining a large niche width with a small capture efficiency will lead to an even stronger increase in predator-prey size ratio, which may explain the large size ratio often encountered in filter feeders. These mechanisms might also provide an explanation for the tendency of the predator-prey size ratio to decrease with trophic level (Cohen et al. 2003), as predators at higher trophic levels may more often be raptorial feeders than filter feeders.

## 6. Conclusions

A size-dependent functional response was developed and combined with body-size scaling relationships from DEB theory to establish a physiologically motivated eco-evolutionary model of adaptations in the body sizes and prey-size preferences of predators. To obtain a realistic coexistence set for feasible predator-prey size combinations, we included capture times that depend on predator-prey size ratios. The resulting model exhibits many features, both ecological and evolutionary, that match empirical observations, such as the triangular distribution of predator-prey size combinations, the island rule, dwarfing, and the difference in predator-prey size ratio between filter feeders and raptorial feeders.

The coexistence set predicted by our model accommodates a wide range of predator-prey size ratios. By contrast, the evolutionary outcomes in the simplest versions of our model, in which a single predator adapts either to a single prey or to a range of prey, imply a fixed predator-prey size ratio. Even though such a fixed size ratio often exists within trophic and taxonomic groups, it certainly does not apply across these groups. We therefore introduced and examined various factors that may help explain variation in predator-prey size ratios. These factors can be organized into three different classes (Figure 6).

First, some factors may change the size ratio predicted for single-predator adaptation (Figure 6a). Therefore, these factors can have a large impact on observed patterns of predator-prey size combinations. Examples include changes in physiology and feeding mode, but also changes in food abundance. Within taxonomic or trophic groups, organisms often possess a relatively similar physiology, which may therefore explain the constant size-ratio that is observed within such groups. It should be noted that factors in this class, in contrast to those listed further below, may also affect the boundaries of the coexistence set. Yet, on the logarithmic scale used in Figures 1 to 3, the resultant lower boundaries of the coexistence set lie close to each other for a relatively large range of parameter values.

Second, there are other factors that cause predators to change their body size and prey-size preference without changing their predator-prey size ratio (Figure 6b). These include, for example, changes in the range of available prey sizes. Also, the patterns of size combinations resulting from resource competition conform to a fixed predator-prey size ratio. In addition, our analysis has demonstrated that competition for resources induces differentiation, rather than mere shifts, in predator body sizes and prey-size preferences. Changes in the available range of prey sizes and resource competition may thus explain the range of predator body



sizes and prey-size preferences observed in nature, but cannot explain the large variation in predator-prey size ratios.

Third, some factors may systematically induce organisms to depart from the predator-prey size ratio predicted for single-prey-single-predator adaptation (Figure 6c). We have found that predation among predators, as well as interference competition, can cause this effect, by giving an additional advantage to large body sizes. As such, these processes may provide an explanation for the tendency of natural selection to produce large-bodied species (Cope's rule). Factors from this third class also help us understand the diversity of predator-prey size ratios encountered in nature.

Distinguishing which of these types of processes is causing the variation in specific empirical predator-prey size combinations will not be easy. Several parameters and processes have similar, or compensatory, effects that are difficult to separate, even in experiments. For example, in most cases it will be problematic to assess the evolutionary outcome of single-prey-single-predator adaptation. This is because the organism will usually have adapted evolutionarily to its specific environment, which typically includes predation and competition. These limitations should be taken into account when trying to explain empirical predator-prey patterns, or when measuring predator-prey size ratios in experimental setups.

### **Acknowledgments**

T.A. Troost thanks the International Institute for Applied Systems Analysis (IIASA) in Austria for providing the possibility of a three-month stay during which the basis for this paper was laid out, and the Netherlands Organization for Scientific Research (NWO) for financing this stay. The authors are very grateful for the data kindly provided by J. Cohen, S. Pimm, P. Yodzis, and J. Saldaña, previously published in Cohen et al. (1993), and for their approval to use them in Figure 2. We also would like to thank M. Boer, O. Diekmann, F. Kelpin, and M. Kirkilionis for helpful discussions on delay differential equations. Furthermore, we would like to thank two anonymous referees for their comments which have considerably improved the paper. U. Dieckmann gratefully acknowledges financial support by the European Marie Curie Research Training Network FishACE (Fisheries-induced Adaptive Changes in Exploited Stocks), funded by the European Communitys Sixth Framework Programme.

### Appendix: Derivation of invasion fitness

In this appendix we show that for determining the invasion fitness of the DDE system (12) one can use an ODE formulation without delay. For this purpose, below we derive the invasion fitness of a mutant predator trying to invade a given resident population of predators. For determining the coexistence set a formulation without delay can be derived as well, which we will not demonstrate explicitly, since that derivation is very similar to the one presented below.

We start from the DDE system (12), consisting of a prey population  $x_1$  and a resident predator population  $x_{A,r}$ , and introduce a mutant predator population  $x_{A,m}$  according to Equation (14). For the sake of clarity, we consider only a single prey population and leave out the tildes that denote scaled parameters in the main text. The derivation of the invasion fitness for multiple prey requires just a few adjustments, as is explained at the end of this appendix. The resulting full system is given by

$$\frac{dx_1(\tau)}{d\tau} = (x_{r,1} - x_1(\tau))D - I_{1,r}f_{1,r}(\tau)x_{A,r}(\tau) - I_{1,m}f_{1,m}(\tau)x_{A,m}(\tau), \quad (21a)$$

$$\frac{dx_{A,r}(\tau)}{d\tau} = R_r(\tau - a_{b,r}) \exp(-h_r a_{b,r})x_{A,r}(\tau - a_{b,r}) - h_r x_{A,r}(\tau), \quad (21b)$$

$$\frac{dx_{A,m}(\tau)}{d\tau} = R_m(\tau - a_{b,m}) \exp(-h_m a_{b,m})x_{A,m}(\tau - a_{b,m}) - h_m x_{A,m}(\tau). \quad (21c)$$

We assume that there is a stable equilibrium of the prey-resident system, Equations (21) for  $x_{A,m}(\tau) = 0$ , at which the resident predator population has positive density. We confirmed this assumption numerically for the coexistence set shown in Figure 1 using the default parameter values given in Table 2.

The subsequent analysis can be outlined as follows. In order to derive the mutant's invasion fitness, we study the stability of the full system after the mutant has been introduced at the prey-resident equilibrium. The full prey-resident-mutant system above is then linearized around this equilibrium, and the characteristic equation of the resultant linear system is analyzed. When the real parts of all roots of this equation are negative, the resident is stable and the mutant cannot invade. By contrast, when the dominant root is positive, the resident is unstable and the mutant can invade. In particular, we will determine the combinations of trait values at which this stability changes.

Below, a superscripted asterisk indicates that the considered variable is at equilibrium under constant environmental conditions. We now introduce new variables that denote dis-

placements from this equilibrium,

$$\begin{aligned}\xi_1 &= x_1 - x_1^*, \\ \xi_{A,r} &= x_{A,r} - x_{A,r}^*, \\ \xi_{A,m} &= x_{A,m} - x_{A,m}^*.\end{aligned}\tag{22}$$

The linearized model at equilibrium then reads

$$\begin{aligned}\frac{d\xi_1(\tau)}{d\tau} &= -\xi_1(\tau)D - I_{1,r}(\xi_1(\tau))\frac{df_{1,r}}{dx_1}(x_1^*)x_{A,r}^* + f_{1,r}(x_1^*)\xi_{A,r}(\tau) \\ &\quad - I_{1,m}(\xi_1(\tau))\frac{df_{1,m}}{dx_1}(x_1^*)x_{A,m}^* + f_{1,m}(x_1^*)\xi_{A,m}(\tau),\end{aligned}\tag{23a}$$

$$\frac{d\xi_{A,r}(\tau)}{d\tau} = (\xi_1(\tau - a_{b,r}))\frac{dR_r}{dx_1}(x_1^*)x_{A,r}^* + R_r(x_1^*)\xi_{A,r}(\tau - a_{b,r}) \exp(-h_r a_{b,r}) - h_r \xi_{A,r}(\tau),\tag{23b}$$

$$\frac{d\xi_{A,m}(\tau)}{d\tau} = (\xi_1(\tau - a_{b,m}))\frac{dR_m}{dx_1}(x_1^*)x_{A,m}^* + R_m(x_1^*)\xi_{A,m}(\tau - a_{b,m}) \exp(-h_m a_{b,m}) - h_m \xi_{A,m}(\tau).\tag{23c}$$

In the following we use the shorthand notations  $R_r^* = R_r(x_1^*)$  and  $R_m^* = R_m(x_1^*)$ .

Since we are interested in the invasion by a rare mutant population, we take  $x_{A,m}^* = 0$ . Then the matrix  $\mathcal{P}$ , defined by

$$\mathcal{P} \begin{pmatrix} \zeta_1 \\ \zeta_{A,r} \\ \zeta_{A,m} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},\tag{24}$$

is obtained by substituting  $\xi_i$  in Equations (23) by  $\xi_i = \zeta_i \exp(\lambda\tau)$ ,  $i = 1, (A, r), (A, m)$  and division by  $\exp(\lambda\tau) > 0$ ,

$$\mathcal{P} = \left( \begin{array}{cc|c} \mathcal{J}_1 & & -I_{1,m}f_{1,m}(x_1^*) \\ & & 0 \\ \hline & & \\ \hline 0 & 0 & \mathcal{J}_2 \end{array} \right).\tag{25}$$

The  $2 \times 2$  matrix  $\mathcal{J}_1$  is given by

$$\mathcal{J}_1 = \begin{pmatrix} -(\lambda + h_r) - I_{1,r}\frac{df_r}{dx_1}(x_1^*)x_{A,r}^* & -I_{1,r}f_{1,r}(x_1^*) \\ \exp(-(\lambda + h_r)a_{b,r})\frac{dR_r}{dx_1}(x_1^*)x_{A,r}^* & R_r^* \exp(-(\lambda + h_m)a_{b,r}) - (\lambda + h_m) \end{pmatrix}\tag{26}$$

and the  $1 \times 1$  matrix  $\mathcal{J}_2$  by

$$\mathcal{J}_2 = R_m^* \exp(-(h_m + \lambda)a_{b,m}) - (\lambda + h_m).\tag{27}$$

The characteristic equation is obtained by the requirement that the determinant of the matrix  $\mathcal{P}$  be equal to zero. Then the  $\zeta_i$  play the role of eigenvector components and the complex number  $\lambda$  plays the role of eigenvalue, which is now a root of the characteristic equation.

Since the mutant is assumed to be rare, the determinant of  $\mathcal{P}$  factorizes, being given by the product of  $\det \mathcal{J}_1$  and  $\det \mathcal{J}_2 = \mathcal{J}_2$ , with these two factors corresponding to the two decoupled systems: the prey-resident system without the mutant (i.e.,  $x_{A,m}^* = 0$ ), described by  $\mathcal{J}_1$ , and the growth rate of the mutant population, described by  $\mathcal{J}_2$ .

The first factor yields the characteristic equation of the prey-resident system,  $\det \mathcal{J}_1 = 0$ . This characteristic equation belongs to the eigenvalue problem for the set of one ODE and one DDE given by Equation (23a), without the last term, and Equation (23b), evaluated at the equilibrium of the prey-resident system.

The second factor yields the characteristic equation  $\det \mathcal{J}_2 = \mathcal{J}_2 = 0$  of the first-order linear homogeneous DDE (Equation 23c) describing the specific growth rate of the mutant population. The expression for  $\mathcal{J}_2$  in Equation (27) is of a form discussed extensively by Diekmann et al. (1995, page 312). For this case, the complex roots of the characteristic equation can be obtained analytically.

The function  $\mathcal{J}_2(\lambda)$  with  $\lambda \in \mathbf{R}$  is monotonically decreasing,  $d\mathcal{J}_2/d\lambda < 0$ . Therefore there is one unique real root  $\lambda_0$ . Since  $\mathcal{J}_2(0) = R_m^* \exp(-h_m a_{b,m}) - h_m$ , the real eigenvalue equals zero,  $\lambda_0 = 0$ , if and only if  $R_m^* \exp(-h_m a_{b,m}) = h_m$ . Thus, Equation (27) has exactly one positive real solution,  $\lambda_0 > 0$ , when  $R_m^* \exp(-h_m a_{b,m}) > h_m$  and exactly one negative real solution,  $\lambda_0 < 0$ , when  $R_m^* \exp(-h_m a_{b,m}) < h_m$ . Further, (Driver 1977, page 321) showed that equations of this form have infinitely many complex roots. Let  $\lambda_k = \mu_k + i\omega_k$ ; then substitution of this into the characteristic equation  $\mathcal{J}_2 = 0$  and separately equating real and imaginary parts gives

$$\mu_k = \exp(-\mu_k a_{b,m}) R_m^* \exp(-h_m a_{b,m}) \cos(a_{b,m} \omega_k) - h_m, \quad (28)$$

$$\omega_k = -\exp(-\mu_k a_{b,m}) R_m^* \exp(-h_m a_{b,m}) \sin(a_{b,m} \omega_k). \quad (29)$$

Clearly, if Equation (29) holds for  $\omega_k$ , it holds also for  $-\omega_k$ , so the complex conjugate  $\lambda_k^* = \mu_k - i\omega_k$  is also a root of the characteristic equation. Furthermore, the unique real root  $\lambda_0$  is the dominant eigenvalue, i.e., the real parts of all other roots are smaller than  $\lambda_0$ . This can be seen as follows. Comparison of Equation (28) with the characteristic equation for

$\lambda_0$  gives

$$\lambda_0 - \mu_k = (1 - \exp((\lambda_0 - \mu_k)a_{b,m}) \cos(a_{b,m}\omega_k)) R_m^* \exp(-h_m a_{b,m}) . \quad (30)$$

Suppose that  $\cos(a_{b,m}\omega_k) = 1$ , then  $\sin(a_{b,m}\omega_k) = 0$ , and hence  $\omega_k = 0$ , which contradicts the fact that  $\lambda_k = \mu_k + i\omega_k$  has non-zero imaginary part. We can thus conclude that  $\cos(a_{b,m}\omega_k) < 1$ . Now assume that  $\lambda_0 - \mu_k \leq 0$ , then, with  $R_m^* > 0$  (since  $R_m^* \approx R_r^* > 0$  due to small mutational steps), Equation (30) implies  $1 \leq \exp((\lambda_0 - \mu_k)a_{b,m}) \cos(a_{b,m}\omega_k)$ , and also this leads to a contradiction. This shows that  $\text{Re}(\lambda_k) < \lambda_0$ ,  $k = 1, 2, \dots$ , or in other words: the real eigenvalue  $\lambda_0$  is the dominant root of the characteristic equation  $\det \mathcal{J}_2 = 0$ .

We had mentioned above that the prey-resident system has a positive stable equilibrium for the default parameter values given in Table 2. Under these circumstances, the real parts of the eigenvalues of  $\mathcal{J}_1$  are strictly negative. Thus, the dominant eigenvalue  $\lambda_0$  of  $\mathcal{J}_2$  will also be the dominant eigenvalue of  $\mathcal{P}$ , if this  $\lambda_0$  exceeds the largest real part of the eigenvalues of  $\mathcal{J}_1$ . Hence, for  $\det \mathcal{J}_2 = 0$ , that is, for  $R_m^* \exp(-h_m a_{b,m}) = h_m$ , the dominant eigenvalue of  $\mathcal{P}$  will equal  $\lambda_0$  and thus zero. At trait values for which this holds, the prey-resident-mutant system changes stability, so that the prey-resident system becomes invadable by the mutant predator.

Now suppose that the real eigenvalue  $\lambda_0$  is positive but small. Then the characteristic equation of  $\mathcal{J}_2$  gives

$$\begin{aligned} \lambda_0 &= R_m^* \exp(-(\lambda_0 + h_m)a_{b,m}) - h_m \\ &= (1 - \lambda_0 a_{b,m} + \frac{1}{2} \lambda_0^2 a_{b,m}^2 + \dots) R_m^* \exp(-h_m a_{b,m}) - h_m, \end{aligned}$$

so that, for  $\lambda_0 a_{b,m} \ll 1$ , we have

$$\lambda_0 = R_m^* \exp(-h_m a_{b,m}) - h_m. \quad (31)$$

Consequently, the rate  $\lambda_0$  is the invasion fitness of the mutant predator at the equilibrium of the prey-resident system, ( $x_1^* > 0$ ,  $x_{A,r}^* > 0$ ,  $x_{A,m}^* = 0$ ).

We have thus shown that, if  $\lambda_0 a_{b,m} \ll 1$ , which holds for small mutational steps, the invasion fitness can be determined by a formulation without delay, corroborating our approach in the main text (Equation 15). The rare mutant ( $x_{A,m} \rightarrow 0$ ) will be able to invade the stable prey-resident system if and only if  $R_m^* \exp(-h_m a_{b,m}) > h_m$ . The biological interpretation of this inequality is clear: the mutant's effective birth rate has to exceed the dilution rate. After

successful invasion, the mutant generally replaces the resident (Geritz et al. 2002); around evolutionary branching points they can coexist, leading to a dimorphic predator population (Metz et al. 1992, 1996; Geritz et al. 1997, 1998).

For the (ecological) stability at the boundaries of the coexistence set a formulation without delay can be derived as well. This derivation is very similar to that of the invasion fitness explained above, but simpler, as no mutants are considered but only the prey and resident predator populations. The resulting condition fulfilled at the boundaries of the coexistence set is given by  $R^* \exp(-ha_b) = h$ .

Considering multiple prey populations instead of a single one will affect system (21) in two ways. First, the dynamics of each prey population are described by a separate equation, such that for  $n$  prey populations, the full system will consist of  $n + 2$  equations. Second, the prey populations will affect the growth rate  $R$  (Equation 13) of the predators (both residents and mutants) through their functional response  $f$  (Equation 6). The derivation of the invasion fitness itself, however, is largely analogous to that shown above. The determinant of the matrix  $\mathcal{P}$  is still factorizable, and remains given by the product of  $\det \mathcal{J}_1$  and  $\det \mathcal{J}_2$ .  $\mathcal{J}_2$  is still given by Equation (27), adjusted for multiple prey through  $f$  in  $R$ .  $\mathcal{J}_1$  will now be a  $(n + 1) \times (n + 1)$  matrix, which corresponds to the system of the resident predator and the  $n$  prey populations without the mutant predator. Supported by the simulation results, we again assume that the system without the mutant is stable. It is then easy to see that the invasion fitness for multiple prey resembles that for a single prey (Equation 31), adjusted through  $f$  in  $R$ .

## REFERENCES

- Aljetlawi, A. A., Sparrevik, E., and Leonardsson, K. (2004). Prey-predator size-dependent functional response: Derivation and rescaling to the real world. *Journal of Animal Ecology*, 73(2):239–252.
- Alver, M. O., Alfredsen, J. A. and Olsen, Y. (2006). An individual-based population model for rotifer (*Brachionus plicatilis*) cultures. *Hydrobiologia*, 560:93–208.
- Benton, M. J. (2002). *Cope's rule*. In: M. Pagel (Ed). *Encyclopedia of Evolution*. Oxford University Press, Oxford, pages 185–186.
- Bergmann, C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihre Grösse. *Göttinger Studien*, 3:595–708.
- Brown, J. H., Marquet, P. A., and Taper, M. L. (1993). Evolution of body size: Consequences of an energetic definition of fitness. *American Naturalist*, 142(4):573–584.
- Case, T. J. (1978). Endothermy, and parental care in the terrestrial vertebrates. *American Naturalist*, 112(987):861–874.
- Cohen, J. E. (1989). *Food webs and community structure*. In: J. Roughgarden, R. M. May and S. A. Levin (Eds). *Perspectives on Ecological Theory*. Princeton University Press, Princeton, pages 181–202.
- Cohen, J. E., Jonsson, T., and Carpenter, S. R. (2003). Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, 100(4):1781–1786.
- Cohen, J. E. and Newman, C. M. (1985). A stochastic theory of community food webs 1. Models and aggregated data. *Proceedings of the Royal Society of London B-Biological Sciences*, 224(1237):448–461.
- Cohen, J. E., Pimm, S. L., Yodzis, P., and Saldana, J. (1993). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62(1):67–78.
- Combes, C. (2001). *Parasitism; the ecology and evolution of intimate interactions*. University of Chicago Press.
- Cope, E. D. (1896). *The primary factors of organic evolution*. The Open Court Publishing Company, Chicago.

- Dieckmann, U. (1997). Can adaptive dynamics invade? *Trends in Ecology and Evolution*, 12(4):128–131.
- Dieckmann, U. and Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic processes. *Journal of Mathematical Biology*, 34(5–6):579–612.
- Diekmann, O., van Gils, S. A., Verduyn Lunel, S. M., and Walther, H.-O. (1995). *Delay Equations: Functional-, complex- and nonlinear analysis*, Volume 110 of *Applied Mathematical Sciences*. Springer-Verlag, New York.
- Driver, R. D. (1977). *Ordinary and Delay Differential Equations*, Volume 20 of *Applied Mathematical Sciences*. Springer-Verlag, New York.
- Ellis, T. and Gibson, R. N. (1997). Predation of 0-group flatfishes by 0-group cod: Handling times and size-selection. *Marine Ecology - Progress Series*, 149(1-3):83–90.
- Forsman, A. (1996). Body size and net energy gain in gape-limited predators: A model. *Journal of Herpetology*, 30(3):307–319.
- Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A. and Parvinen, K. (2002). Invasion dynamics and attractor inheritance. *Journal of Mathematical Biology*, 44(6):548560.
- Geritz, S. A. H., Kisdi, É., Meszéna, G. and Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12(1):35–57.
- Geritz, S. A. H., Metz, J. A. J., Kisdi, É., and Meszéna, G. (1997). Dynamics of adaptation and evolutionary branching. *Physical Review Letters*, 78(10):2024–2027.
- Gittleman, J. L. (1985). Carnivore body size: Ecological and taxonomic correlates. *Oecologia*, 67(4):540–554.
- Hansen, B., Bjornsen, P. K., and Hansen, P. J. (1994). The size ratio between planktonic predators and their prey. *Limnology and Oceanography*, 39(2):395–403.
- Husseman, J. S., Murray, D. L., Power, G., Mack, C., Wenger, C. R., and Quigley, H. (2003). Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos*, 101(3):591–601.



- Karpouzi, V. and Stergiou, K. I. (2003). The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology*, 62(6):1353–1365.
- Kooi, B. W. and Kooijman, S. A. L. M. (1997). Population dynamics of rotifers in chemostats. *Nonlinear Analysis, Theory, Methods & Applications*, 30(3):1687–1698.
- Kooi, B. W. and Kooijman, S. A. L. M. (1999). Discrete event versus continuous approach to reproduction in structured population dynamics. *Theoretical Population Biology*, 56(1):91–105.
- Kooijman, S. A. L. M. (1986). Energy budgets can explain body size relations. *Journal of Theoretical Biology*, 121:269–282.
- Kooijman, S. A. L. M. (2000). *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press.
- Kooijman, S. A. L. M. (2001). Quantitative aspects of metabolic organization; a discussion of concepts. *Philosophical Transactions of the Royal Society B–Biological Sciences*, 356(1407):331–349.
- Kristiansen, J. N., Fox, T., and Nachman, G. (2000). Does size matter? Maximising nutrient and biomass intake by shoot size selection amongst herbivorous geese. *Ardea*, 88(2):119–125.
- Loeuille, N. and Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America* 102(16):5761–5766.
- Manatunge, J. and Asaeda, T. (1998). Optimal foraging as the criteria of prey selection by two centrarchid fishes. *Hydrobiologica*, 391(1-3):223–240.
- Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, 10(1):105–108.
- Mayr, E. (1963). *Animal Species and Evolution*. Harvard University Press, Cambridge, Mass.
- Mehner, T., Plewa, M., Hulsmann, S., and Worischka, S. (1998). Gape-size dependent feeding of age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*) on daphnia galeata. *Archiv für Hydrobiologie*, 142(2):191–207.

- Memmott, J., Martinez, N. D., and Cohen, J. E. (2000). Predators, parasitoids and pathogens: Species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*, 69(1):1–15.
- Metz, J. A. J., Nisbet, R. M. and Geritz, S. A. H. (1992). How should we define ‘fitness’ for general ecological scenarios? *Trends in Ecology and Evolution*, 7(6):198–202.
- Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A. and van Heerwaarden, J. S. (1996). Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S. J. and Verduyn Lunel, S. M. (Eds.). *Stochastic and Spatial Structures of Dynamical Systems*. KNAW Verhandelingen, Amsterdam, pages 183–231.
- Neubert, M. G., Blumenshine, S. C., Duplisea, D. E., Jonsson, T., and Rashleigh, B. (2000). Body size and food web structure: Testing the equiprobability assumption of the cascade model. *Oecologia*, 123(2):241–251.
- Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, New York.
- Rincon, P. A. and Loboncervia, J. (1995). Use of an encounter model to predict size-selective predation by a stream-dwelling cyprinid. *Freshwater Biology*, 33(2):181–191.
- Rytkonen, S., Kuokkanen, P., Hukkanen, M., and Huhtala, K. (1998). Prey selection by sparrowhawks *Accipiter nisus* and characteristics of vulnerable prey. *Ornis Fennica*, 75(2):77–87.
- Svensson, J. E. (1997). Fish predation on *Eudiaptomus gracilis* in relation to clutch size, body size, and sex: A field experiment. *Hydrobiologica*, 344(1–3):155–161.
- Turesson, H., Persson, A., and Bronmark, C. (2002). Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. *Ecology of Freshwater Fish*, 11(4):223–233.
- Van Valen, L. (1973). Pattern and the balance of nature. *Evolutionary Theory*, 1:31–49.
- Vezina, A. F. (1985). Empirical relationships between predator and prey size among terrestrial vertebrate predators. *Oecologia*, 67(4):555–565.

- Warren, P. H. and Lawton, J. H. (1987). Invertebrate predator-prey body size relationships: An explanation for upper triangular food webs and patterns in food web structure? *Oecologia*, 74(2):231–235.
- Williams, R. J. and Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, 404(6774):180–183.
- Yodzis, P. and Innes, S. (1992). Body size and consumer-resource dynamics. *American Naturalist*, 139(6):1151–1175.

Table 1: Parameters and state variables of the model.

Symbol	Dimension	Meaning
<i>Physiological parameters</i>		
$a_b, a_A$	$T$	Embryo-development time and egg-production time; $a_b = 3/k_E$
$e, \hat{e}$	–	Scaled energy density, of adult and of newborn individuals; $e = [E]/[E_{\max}] = f$
$[E], [E_{\max}], [E_{\max}]_{\text{ref}}$	$EL^{-3}$	Volume-specific energy density; actual, maximum, and reference
$g, g^+$	–	Energy investment ratio for biomass and embryo growth; $g^+ = g + \frac{3}{4}gk_M/v$
$h$	$T^{-1}$	Mortality rate
$k_E$	$T^{-1}$	Specific energy conductance; $k_E = v/\ell_A$
$k_M$	$T^{-1}$	Maintenance rate coefficient
$R$	$T^{-1}$	Reproduction rate
$\alpha$	–	Proportion of the maximum size that is reached; $\alpha = \ell_A/\ell_{\max}$
$v$	$LT^{-1}$	Energy conductance
<i>Trophic parameters</i>		
$b, b_0$	$l^3L^{-3}T^{-1}$	Volume-specific encounter rate and encounter rate coefficient
$D$	$T^{-1}$	Dilution rate
$f, f_i$	–	Functional response; overall, and with respect to prey population $i$
$I_i$	$T^{-1}$	Maximum volume-specific intake rate for prey population $i$
$\ell_i, \ell_{\max}, \ell_{\text{ref}}$	$L$	Length of individuals of prey population $i$ ; maximum length of predator; reference length
$t_g, t_c, t_h$	$T$	Ingestion, capture, and handling time
$[t_h], [t_{h,i}], [t_h]_{\text{ref}}$	$T$	Volume-specific handling time: actual, with respect to prey population $i$ , and minimum.
$[t_{g,0}], [t_{c,0}]$	$T$	Coefficients for volume-specific ingestion and capture time
$X_{r,i}, X_{r,0}$	$L^3l^{-3}$	Incoming prey density; function, and scaling coefficient
$\delta$	$L$	Distance between the successive lengths of incoming prey-size distribution
$\mu$	$L$	Mean length of incoming prey-size distribution
$\sigma_p, \sigma$	–	Standard deviation; of attack probability (niche width), and of incoming prey-size distribution
$\rho_a, \rho_s$	–	Attack probability and capture efficiency
<i>Ecological state variables</i>		
$X_A, X_i$	$L^3l^{-3}$	Structural volume density of (adult) predators and of prey population $i$
<i>Evolutionary state variables</i>		
$\ell_A$	$L$	Adult length of predator
$\ell_P$	$L$	Prey-size preference of predator

Dims:  $T$ , time;  $L$ , length of individual;  $l$ , length of reactor;  $E$ , energy.

Table 2: Default parameter values.

Parameter	Default value
$\tilde{b}_0$	1000
$\tilde{D}$	0.1
$\tilde{\ell}_{\text{ref}}$	1
$[\tilde{t}_{c,0}]$	3.5
$[\tilde{t}_{g,0}]$	0.77
$\alpha$	0.1
$\sigma_{\text{p}}$	0.05
$\sigma$	0.25
$\rho_s$	1
$\tilde{\mu}$	0.5

Tildes indicate that parameters are scaled by  $v$ ,  $k_{\text{M}}$  and/or  $X_{\text{r},0}$  to make them dimensionless.

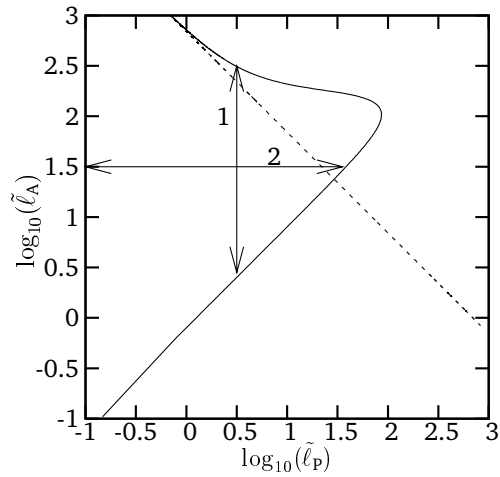


Fig. 1.— Coexistence set of the investigated predator-prey system. Combinations of scaled predator body size  $\tilde{\ell}_A$  (vertical) and prey-size preference  $\tilde{\ell}_P$  (horizontal) are shown logarithmically, assuming that the preferred prey size equals the one available prey size ( $\tilde{\ell}_P = \tilde{\ell}_1$ ). The dashed curve depicts the boundary of this coexistence set when only ingestion and encounter times are considered, while the continuous curve shows this boundary when capture times are considered as well. The two arrows indicate the graph's two possible interpretations: (1) the feasible range of predator body sizes for a given prey size, and (2) the feasible range of prey-size preferences for a given predator size.

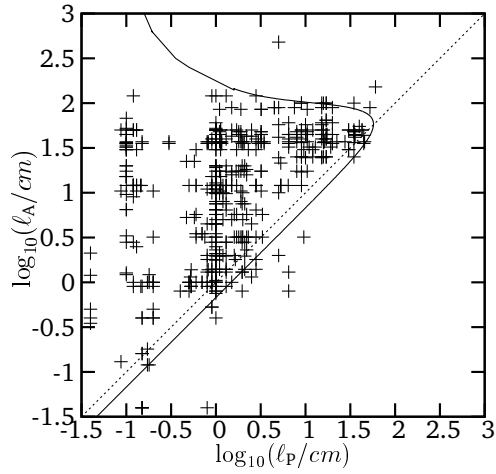


Fig. 2.— Comparison of the coexistence set predicted by our model (continuous curve) with empirical data presented by Cohen et al. (1993). The logarithm of the length of the predator is plotted against the logarithm of the length of the prey, with both lengths being expressed in centimeters. Along the dotted line, body sizes of prey and predator are equal. The dimensionless variables  $\tilde{\ell}_A$  and  $\tilde{\ell}_P$  were translated back into lengths using the two relevant scaling parameters,  $k_M = 1.44 \text{ d}^{-1}$  and  $v = 0.3 \text{ cm d}^{-1}$ ; the dilution rate was set to  $\tilde{D} = 0.05$ .

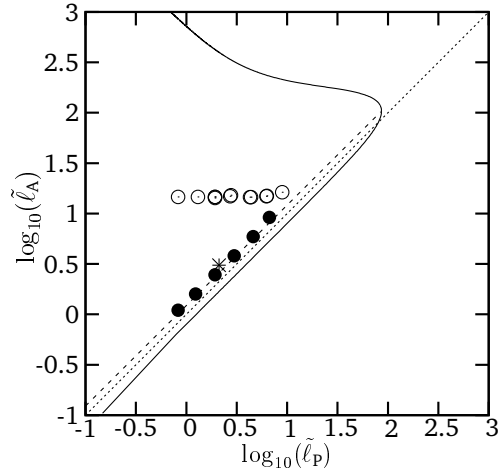


Fig. 3.— Evolutionary outcomes of scaled predator body size  $\tilde{\ell}_A$  and prey-size preference  $\tilde{\ell}_P$ . The continuous curve depicts the boundary of the coexistence set, while the dotted line depicts the diagonal along which predator size and prey-size preference are equal. The dashed line shows the outcome of single-trait predator evolution in  $\tilde{\ell}_A$ , for a single prey size, with  $\tilde{\ell}_P = \tilde{\ell}_1$ . The asterisk indicates the initial evolutionary equilibrium (and primary evolutionary branching point) of two-trait evolution in the predator when considering a range of available prey sizes. The filled circles show the composition of the predator community after evolutionary branching (deterministic evolution), while the open circles depict this composition when predation among predators was also taken into account (stochastic evolution).



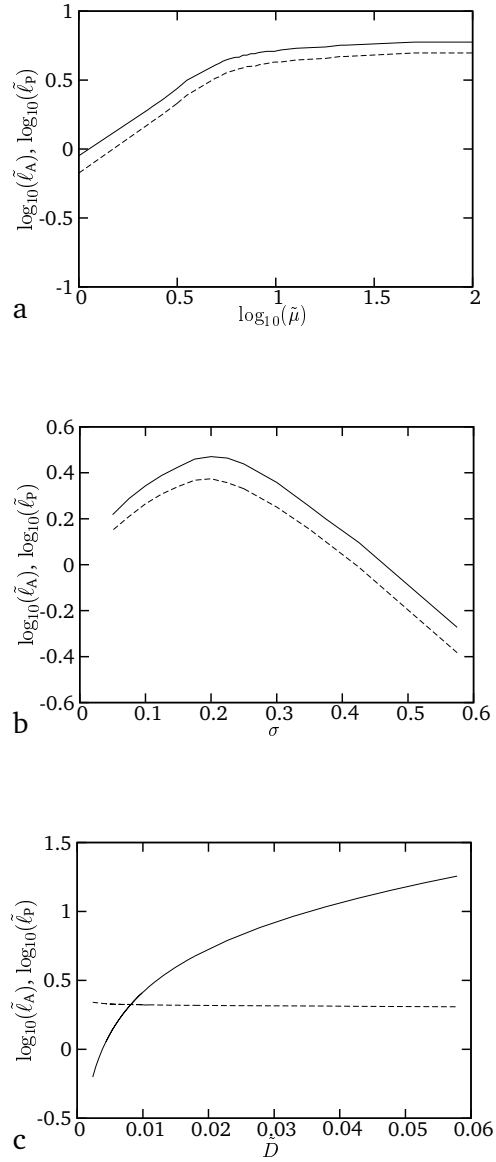


Fig. 4.— Effects of environmental parameters on the evolutionary outcomes of scaled predator body size  $\tilde{\ell}_A$  (continuous curve) and prey-size preference  $\tilde{\ell}_P$  (dashed curve). The three panels show the evolutionary equilibrium values (a) for a range of means  $\tilde{\mu}$  of the available prey-size distribution, (b) for a range of standard deviations  $\sigma$  of this distribution, and (c) for a range of dilution rates  $\tilde{D}$ .

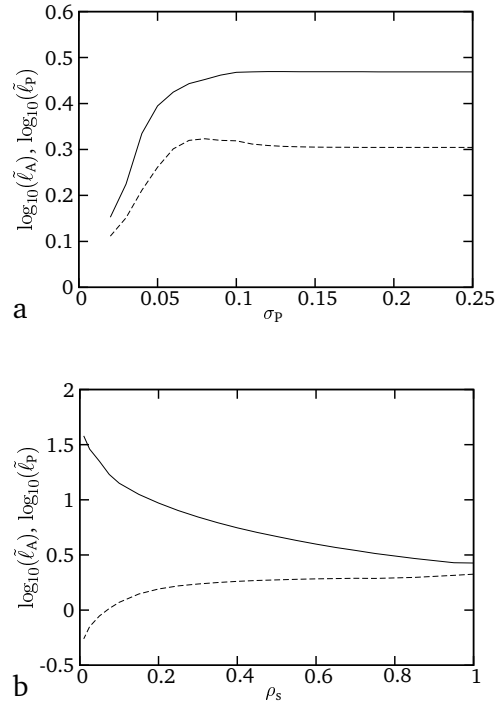


Fig. 5.— Effects of ecological parameters on the evolutionary outcomes of scaled predator body size  $\tilde{l}_A$  (continuous curve) and prey-size preference  $\tilde{l}_p$  (dashed curve). The two panels show the evolutionary equilibrium values (a) for a range of niche widths  $\sigma_p$  and (b) for a range of capture efficiencies  $\rho_s$ .

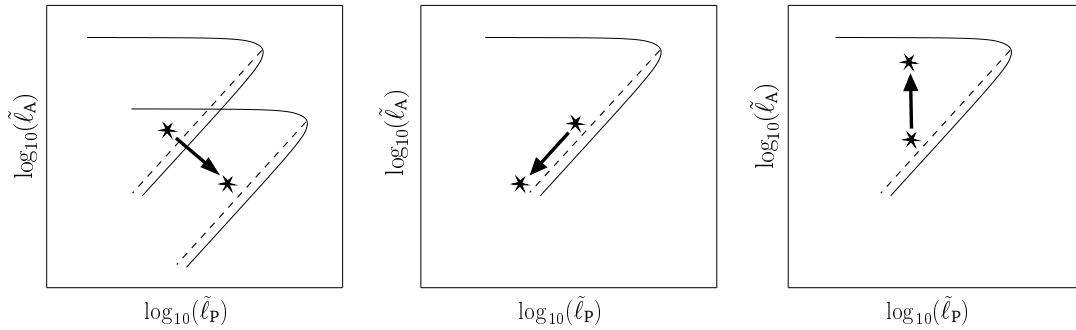


Fig. 6.— Three different types of change in evolved predator-prey patterns. Continuous curves delineate the boundaries of the coexistence set, dashed lines show the outcomes of single-trait evolution, and asterisks indicate the evolutionary outcome of two-trait predator evolution when a range of prey types is present. Arrows depict changes in the predator’s two adaptive traits  $\tilde{l}_A$  (vertical) and prey-size preference  $\tilde{l}_P$  (horizontal): (a) the expected outcome of evolution in predator body size and predator-prey size ratio is changed, together with the coexistence set; (b) predator body size evolves, while the predator-prey size ratio remains the same; (c) the predator evolves away from the body size and size ratio predicted by single-trait predator evolution.