

University of Groningen

Foraging in a spatially patterned world

Klaassen, Raymond Hendrikus Gerardus

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2006

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Klaassen, R. H. G. (2006). *Foraging in a spatially patterned world: Migratory swans (Cygnus columbianus) seeking buried pondweed (Potamogeton pectinatus) tubers.* s.n.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Literature cited

- Adler P.B., D.A. Raff and W.K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465-479.
- Alonso J.C., J.A. Alonso, L.M. Bautista and R. Muñoz-Pulido. 1995. Patch use in cranes: a field test of optimal foraging predictions. *Animal Behaviour* 49: 1367-1379.
- Anderson D.J. 1983. Optimal foraging and the traveling salesman. *Theoretical Population Biology* 24: 145-159.
- Arditi R. and B. Dacorogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist* 131: 837-846.
- Badzinski S.S. 2003. Dominance relations and agonistic behaviour of Tundra Swans (*Cygnus columbianus columbianus*) during fall and spring migration. *Canadian Journal of Zoology* 81: 727-733.
- Barnard C.J. and R.M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour* 29: 543-550.
- Bascompte S. and R.V. Sole. 1998. Spatiotemporal patterns in nature. *Trends in Ecology and Evolution* 13: 173-174.
- Batschelet E. 1981. *Circular statistics in biology*. Academic press, London.
- Bautista L.M., J.C. Alonso and J.A. Alonso. 1995. A field test of ideal free distribution in flock-feeding common cranes. *Journal of Animal Ecology* 64: 747-757.
- Beauchamp G. 2000. Learning rules for social foragers: implications for the producer-scrounger game and ideal free distribution theory. *Journal of Theoretical Biology* 207: 21-35.
- Beauchamp G., M. Bélisle and L.-A. Giraldeau. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *Journal of Animal Ecology* 66: 671-682.
- Beauchamp G. and L.-A. Giraldeau. 1996. Group foraging revisited: information sharing or producer-scrounger game? *American Naturalist* 148: 738-743.
- Beekman J.H., M.R. van Eerden and S. Dirksen. 1991. Bewick's swans *Cygnus columbianus bewickii* utilising the changing resource of *Potamogeton pectinatus* during autumn in the Netherlands. *Wildfowl Supplement* 1: 238-248.
- Beekman J.H., B.A. Nolet and M. Klaassen. 2002. Skipping swans: fuelling rate and wind conditions determine differential use of migratory stopover sites of Bewick's swans *Cygnus bewickii*. *Ardea* 90: 437-460.
- Benhamou S. 1992. Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology* 159: 67-81.
- Bernstein C., A. Kacelnik and J.R. Krebs. 1988. Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology* 57:1007-1026.
- Bond A.B. 1980. Optimal foraging in a uniform habitat: the search mechanism of the green lacewing. *Animal Behaviour* 28: 10-19.
- Bovet P. and S. Benhamou. 1988. Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology* 131: 419-433.
- Brouwer G.A. and L. Tinbergen. 1939. De verspreiding der Kleine Zwanen, *Cygnus b. bewickii* Yarr., in de Zuiderzee, vóór en na de verzoeting. *Limosa* 12: 1-18.

- Brown J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22: 37-47.
- Brown J.S. 2000. Foraging ecology of animals in response to heterogeneous environments. *In*: M.J. Hutchings, E.A. John and A.J.A. Stewart (editors). *The ecological consequences of environmental heterogeneity*. Blackwell Science Ltd., Oxford. pp. 181-214.
- Brown J.S., B.P. Kotler, R.J. Smith and W.O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* 76: 408-415.
- Brown J.S. and W.A. Mitchell. 1989. Diet selection on depletable resources. *Oikos* 54: 33-43.
- Bowler J. 1994. The condition of Bewick's swans *Cygnus columbianus bewickii* in winter as assessed by their abdominal profiles. *Ardea* 82: 241-248.
- Cain M.L. 1989. The analysis of angular data in ecological field studies. *Ecology* 70: 1540-1543.
- Charnov E.L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- Charnov E.L., G.H. Orians and K. Hyatt. 1976. Ecological implications of resource depression. *American Naturalist* 110: 247-259.
- Chase J.M., W.G. Wilson and S.A. Richards. 2001. Foraging trade-offs and resource patchiness: theory and experiments with a freshwater snail community. *Ecology Letters* 4: 304-312.
- Clark C.W. and M. Mangel. 1984. Foraging and flocking strategies: information in an uncertain environment. *American Naturalist* 123: 626-641.
- Clark C.W. and M. Mangel. 1986. The evolutionary advantages of group foraging. *Theoretical Population Biology* 30: 45-75.
- Cramp S. and K.E.L. Simmons. 1977. *Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic*. Vol 1: Ostrich-Ducks. Oxford University Press.
- Cuthill I.C., P. Haccou and A. Kacelnik. 1994. Starlings (*Sturnus vulgaris*) exploiting patches: response to long-term changes in travel time. *Behavioral Ecology* 5: 81-90.
- Dall S.R.X., L.-A. Giraldeau, O. Olsson, J.M. McNamara and D.W. Stephens. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* 20: 187-193.
- de Leeuw J.J. 1996. Diving costs as a component of daily energy budgets in aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted ducks. *Canadian Journal of Zoology* 74: 2131-2142.
- de Leeuw J.J. 1997. Demanding divers. Ecological energetics of food exploitation by diving ducks. PhD Thesis, Groningen University, Groningen, The Netherlands.
- de Leeuw J.J. 1999. Food intake rates and habitat segregation of tufted duck *Aythya fuligula* and scaup *Aythya marila* exploiting zebra mussels *Dreissena polymorpha*. *Ardea* 87: 15-31.
- Dirksen S., J.H. Beekman and T.H. Slagboom. 1991. Bewick's swans *Cygnus columbianus bewickii* in the Netherlands: numbers, distribution and food choice during the wintering season. *Wildfowl* (supplement) 1: 228-237.
- Drent R., C. Both, M. Green, J. Madsen and T. Piersma. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* 103: 274-292.
- Drent R.H. and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

- Drent R.H. and M.R. van Eerden. 1980. Goose flocks and food exploitation: how to have your cake and eat it. Proceedings of the 17th Ornithological Congress, pp 800-806.
- Durant D., H. Fritz, S. Blais and P. Duncan. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *Journal of Animal Ecology* 72: 220-231.
- Ebbinghe B.S. and B. Spaans. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology* 26: 105-113.
- Ely C.R., D.C. Douglas, A.C. Fowler, C.A. Babcock, D.V. Derksen and J.Y. Takekawa. 1997. Migration behavior of the Tundra Swans from the Yukon-Kuskokwim Delta Alaska. *Wilson Bulletin* 109: 679-692.
- Ens B.J. and J.D. Goss-Custard. 1984. Interference among Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *Journal of Animal Ecology* 53: 217-231.
- Fauchald P. 1999. Foraging in a hierarchical patch system. *American Naturalist* 153: 603-613.
- Fierer N. and B. Kotler. 2000. Evidence for micropatch partitioning and effects of boundaries on patch use in two species of gerbils. *Functional Ecology* 14: 176-182.
- Focardi S., P. Marcellini and P. Montanaro. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *Journal of Animal Ecology* 65: 606-620.
- Fortin D. 2002. Optimal searching behaviour: the value of sampling information. *Ecological Modelling* 153: 279-290.
- Fortin D. 2003. Searching behavior and use of sampling information by free-ranging bison (*Bos bison*). *Behavioral Ecology and Sociobiology* 54: 194-203.
- Fritz H., D. Durant and M. Guillemain. 2001. Shape and sources of variations of the functional response of wildfowl: an experiment with mallards, *Anas platyrhynchos*. *Oikos* 93: 488-496.
- Fryxell J.M., J.F. Wilmshurst, A.R.E. Sinclair, D.T. Haydon, R.D. Holt and P.A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters* 8: 328-335.
- Gendron R.P. and J.E.R. Staddon. 1983. Searching for cryptic prey: the effect of search rate. *American Naturalist* 121: 172-186.
- Gill F.B. and L.L. Wolf. 1977. Nonrandom foraging by Sunbirds in a patchy environment. *Ecology* 58: 1284-1296.
- Giraldeau L.-A. and T. Caraco. 2000. *Social foraging theory*. Princeton University Press, New York.
- Giraldeau L.-A., T.J. Valone and J.J. Templeton. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society London series B* 357: 1559-1566.
- Goss-Custard J.D. 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. *In*: R.M. Sibly and R.H. Smith (editors). *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell Science Ltd., Oxford. pp 169-188.
- Goss-Custard J.D., R.A. Stillman, A.D. West, R.W.G. Caldow and S. McGrorty. 2002. Carrying capacity in overwintering migratory birds. *Biological Conservation* 105: 27-41.
- Goss-Custard J.D., R.A. Stillman, R.W.G. Caldow, A.D. West and M. Guillemain. 2003. Carrying capacity in overwintering birds: when are spatial models needed? *Journal of Applied Ecology* 40: 176-187.

- Green R.F. 1980. Bayesian birds: a simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology* 18: 244-256.
- Green R.F. 1984. Stopping rules for optimal foragers. *American Naturalist* 123: 30-43.
- Green R.F. 1987. Stochastic models of optimal foraging. *In*: A.C. Kamil, J.R. Krebs and H.R. Pulliam (editors). *Foraging behavior*. Plenum press, New York. pp. 273-302.
- Green R.F. 1988. Optimal foraging for patchily distributed prey: random search. Technical report 88-2. Department of mathematics & statistics. University of Minnesota, Duluth.
- Green R.F. 1990. Putting ecology back into optimal foraging theory. *Comments Theoretical Biology* 1: 387-410.
- Gross J.E., C. Zank, N.T. Hobbs and D.E. Spalinger. 1995. Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. *Landscape Ecology* 10: 209-217.
- Haccou P., M. Sjerps and E. van der Meijden. 1999. To leave or to stay, that is the question: predictions from models of patch-leaving strategies. *In*: H. Olff, V.K. Brown and R.H. Drent (editors). *Herbivores: between plants and predators*. Blackwell Science Ltd., Oxford. pp. 85-107.
- Haskell J.P., M.E. Ritchie and H. Olff. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* 418: 527-530.
- Hedenström A. and T. Ålerstam. 1998. How fast can birds migrate? *Journal of Avian Biology* 29: 424-432.
- Heinrich B. 1979. Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia* 40: 235-245.
- Hill S., M.T. Burrows and R.N. Hughes. 2002. Adaptive search in juvenile plaice foraging for aggregated and dispersed prey. *Journal of Fish Biology* 61: 1255-1267.
- Hill S.L., M.T. Burrows and R.N. Hughes. 2003. The efficiency of adaptive search tactics for different prey distribution patterns: a simulation model based on the behaviour of juvenile plaice. *Journal of Fish Biology (supplement A)* 63: 117-130.
- Holling C.S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385-398.
- Hulscher J.B. 1982. The oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea* 70: 89-152.
- Hutchings M.J. 1997. The structure of plant populations. *In*: M.J. Crawley (editor). *Plant ecology*. Blackwell Science Ltd. Oxford.
- Illius A.W. and I.J. Gordon. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56: 989-999.
- Iwasa Y., M. Higashi and N. Yamamura. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* 117: 710-723.
- Jonzén N., B.A. Nolet, L. Santamaría and M.G.E. Svensson. 2002. Seasonal herbivory and mortality compensation in a swan-pondweed system. *Ecological Modelling* 147: 209-219.
- Kacelnik A. and C. Bernstein. 1988. Optimal foraging and arbitrary food distributions: patch models gain a lease of life. *Trends in Ecology and Evolution* 3: 251-253.
- Kacelnik A. and A.I. Houston. 1984. Some effects of energy costs on foraging strategies. *Animal Behaviour* 32: 609-614.

- Kareiva P.M. and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* 56: 234-238.
- Kawata M. and H. Agawa. 1999. Perceptual scales of spatial heterogeneity of periphyton for freshwater snails. *Ecology Letters* 2: 210-214.
- Kenkel N.C. 1988. Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.
- Klaassen M. 1995. Water and energy limitations on flight range. *Auk* 112: 260-262.
- Klaassen M., Å. Lindström, H. Møltoft and T. Piersma. 2001. Arctic waders are not capital breeders. *Nature* 413: 794.
- Klaassen R.H.G., B.A. Nolet and D. Bankert. Movement of foraging Tundra swans explained by spatial pattern in cryptic food densities. *Ecology: in press a*.
- Klaassen R.H.G., B.A. Nolet and J. de Fouw. 2006. Intake rate at differently scaled heterogeneous food distributions explained by the ability of tactile-foraging mallard to concentrate foraging effort within profitable areas. *Oikos* 112: 322-331.
- Klaassen R.H.G., B.A. Nolet, J.A. van Gils and S. Bauer. Optimal movement between patches under incomplete information about the spatial distribution of food items. *Theoretical Population Biology, in press b*.
- Knoppien P. and J. Reddingius. 1985. Predators with two modes of searching: a mathematical model. *Journal of Theoretical Biology* 114: 273-301.
- Kokko H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68: 940-950.
- Kooloos J.G.M., A.R. Kraaijeveld, G.E.J. Langenbach and G.A. Zweers. 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves, Anseriformes). *Zoomorphology* 108: 269-290.
- Kotler B.P. and J.S. Brown. 1990. Rates of seed harvest by two species of gerbilline rodents. *Journal of Mammalogy* 71: 591-596.
- Kotliar N.B. and J.A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253-260.
- Krakauer D.C. and M.A. Rodríguez-Gironés. 1995. Searching and learning in a random environment. *Journal of Theoretical Biology* 177: 417-429.
- Krebs C.J. 1989. *Ecological methodology*. Harper and Row Publishers, New York.
- Krebs J.R. and N.B. Davies. 1993. *The evolution of behavioural ecology*. In: J.R. Krebs and N.B. Davies (editors). *Behavioural ecology, an evolutionary approach*. Blackwell Science Ltd., Oxford.
- Lamprecht J. 1986. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). *Behaviour* 96: 28-48.
- Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659-1673.
- Levin S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Li H. and J.F. Reynolds. 1995. On definition and quantification of heterogeneity. *Oikos* 73: 280-284.
- Loonen M., L.W. Bruinzeel, J.M. Black and R.H. Drent. 1999. The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. *Journal of Animal Ecology* 68: 753-768.
- Lovvorn J.R. and M.P. Gillingham. 1996. Food dispersion and foraging energetics: a mechanistic synthesis for field studies of avian benthivores. *Ecology* 77: 435-451.

- MacArthur R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603-609.
- Mangel M. and F.R. Adler. 1994. Construction of multidimensional clustered patterns. *Ecology* 75: 1289-1298.
- Maron J.L. and S. Harrison. 1997. Spatial pattern formation in an insect host-parasitoid system. *Science* 278: 1619-1621.
- McNamara J. 1982. Optimal patch use in a stochastic environment. *Theoretical Population Biology* 21: 269-288.
- Milinski M., P. Boltshauser, L. Büchi, T. Buchwalder, M. Frischknecht, T. Hadermann, R. Künzler, C. Roden, A. Rüetschi, D. Strahm and M. Tognola. 1995. Competition for food in swans: an experimental test of the truncated phenotype distribution. *Journal of Animal Ecology* 64: 758-766.
- Mitchell W.A. 1990. An optimal control theory of diet selection: the effects of resource depletion and exploitative competition. *Oikos* 58: 16-24.
- Moore B.D. and W.J. Foley. 2005. Tree use by koalas in a chemically complex landscape. *Nature* 435: 488-490.
- Morales J.M., D.T. Haydon, J. Frair, K.E. Holsinger and J.M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85: 2436-2445.
- Moran P.A.P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37: 17-23.
- Nummi P. 1993. Food-niche relationships of sympatric mallards and green-winged teals. *Canadian Journal of Zoology* 71: 49-55.
- Nolet B.A. 2004. Overcompensation and grazing optimisation in a swan-pondweed system? *Freshwater Biology* 49: 1391-1399.
- Nolet B.A., V.A. Andreev, P. Clausen, M.J.M. Poot and E.G.J. Wessel. 2001. Significance of the White Sea as a stopover for Bewick's Swans *Cygnus columbianus bewickii* in spring. *Ibis* 143: 63-71.
- Nolet B.A., R.M. Bevan, M. Klaassen, O. Langevoord and Y.G.J.T. van der Heijden. 2002. Habitat switching by Bewick's swans: maximization of average long-term energy gain? *Journal of Animal Ecology* 71: 979-993.
- Nolet B.A. and R.H. Drent. 1998. Bewick's Swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. *Journal of Avian Biology* 29: 574-581.
- Nolet B.A., V.N. Fuld and M.E.C. van Rijswijk. 2006. Foraging costs and accessibility as determinants of giving-up densities in a swan-pondweed system. *Oikos* 112: 353-362.
- Nolet B.A., A. Gyimesi and R.H.G. Klaassen. Prediction of bird-day carrying capacity on a staging site: a test of depletion models. *submitted manuscript*.
- Nolet B.A. and M. Klaassen. 2005. Time and energy constraints in demanding phases of the annual cycle: an example of time limitation in refuelling migratory swans. *Oikos* 111: 302-310.
- Nolet B.A., R.H.G. Klaassen and W.M. Mooij. 2006. The use of a flexible patch leaving rule under exploitative competition: a field test with swans. *Oikos* 112: 342-352.
- Nolet B.A., O. Langevoord, R.M. Bevan, K.R. Engelaar, M. Klaassen, R.J.W. Mulder and S. van Dijk. 2001. Spatial variation in tuber depletion by swans explained by differences in net intake rates. *Ecology* 82: 1655-1667.

- Nolet B.A. and W.M. Mooij. 2002. Search paths of swans foraging on spatially autocorrelated tubers. *Journal of Animal Ecology* 71: 451-462.
- Oaten A. 1977. Optimal foraging in patches: a case for stochasticity. *Theoretical Population Biology* 12: 263-285.
- Olsson O. 2006. Bayesian foraging with only two patch types. *Oikos* 112: 285-297.
- Olsson O. and J.S. Brown. 2006. The foraging benefits of information and the penalty of ignorance. *Oikos* 112: 260-273.
- Olsson O., U. Wiklander, N.M.A. Holmgren and S.G. Nilsson. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. *Oikos* 87: 264-276.
- Olsson O. and N.M.A. Holmgren. 1998. The survival-rate-maximizing policy for Bayesian foragers: wait for good news. *Behavioral Ecology* 9 :345-353.
- Olsson O. and N.M.A. Holmgren. 2000. Optimal Bayesian foraging policies and prey population dynamics – some comments on Rodríguez-Gironés and Vásquez. *Theoretical Population Biology* 57: 369-375.
- Pickett S.T.A. and M.L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269: 331-334.
- Pielou E.C. 1977. *Mathematical ecology*. Wiley-Interscience, New York.
- Pienkowski M.W. 1983. Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour* 31: 244-264.
- Piersma T., R. Hoekstra, A. Dekinga, A. Koolhaas, P. Wolf, P. Battley and P. Wiersma. 1993. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research* 31: 331-357.
- Piersma T., R. van Aelst, K. Kurk, H. Berkhoudt and L.R.M. Maas. 1998. A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proceedings of the Royal Society London series B* 265: 1377-1383.
- Piersma T., J. van Gils, P. de Goeij and J. van der Meer. 1995. Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *Journal of Animal Ecology* 64: 493-504.
- Plowright C.M.S. and S.J. Shettleworth. 1991. Time horizon and choice by pigeons in a prey-selection task. *Animal Learning and Behavior* 19: 103-112.
- Price M.V. and R.A. Correll. 2001. Depletion of seed patches by Merriam's kangaroo rats: are GUD assumptions met? *Ecology Letters* 4: 334-343.
- Prop J., J.M. Black and P. Shimmings. 2003. Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103: 403-414.
- Prop J. and M.J.J.E. Loonen. 1989. Goose flocks and food exploitation: the importance of being first. *Ir: Proceedings of the XIX International Ornithological Congress, Ottawa*. pp: 1878-1887.
- Pyke G.H. 1974. *Studies in the foraging efficiency of animals*. PhD thesis, University of Chicago, USA.
- Pyke G.H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15: 523-575.
- Pyke G.H., H.R. Pulliam and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* 52: 137-154.

- Rietkerk M., S.C. Dekker, P.C. de Ruiter and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305: 1926-1929.
- Ritchie M.E. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology* 12: 309-330.
- Rodriguez-Gironés M.A. and R.A. Vásquez. 1997. Density-dependent patch exploitation and acquisition of environmental information. *Theoretical Population Biology* 52: 32-42.
- Rossi R.E., D.J. Mulla, A.G. Journel and E.H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* 62: 277-314.
- Rowcliffe J.M., R.A. Pettifor and C. Carabone. 2004. Foraging inequalities in large groups: quantifying depletion experienced by individuals in goose flocks. *Journal of Animal Ecology* 73: 97-108.
- Sawada M. 1999. Rookcase: an Excel 97/2000 Visual Basic (VB) add-in for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America* 80: 231-234.
- Santamaría L. 2002. Selective waterfowl herbivory affects species dominance in a submerged plant community. *Archiv für Hydrobiologie* 153: 353-365.
- Santamaría L. and M.A. Rodríguez-Gironés. 2002. Hiding from swans: optimal burial depth of sago pondweed tubers foraged by Bewick's swans. *Journal of Ecology* 90: 303-315.
- Schmidt K.A. and J.S. Brown. 1996. Patch assessment in fox squirrels: the role of resource density, patch size, and patch boundaries. *American Naturalist* 147: 360-380.
- Schoener T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-404.
- Sernland E., O. Olsson, and N.M.A. Holmgren. 2003. Does information sharing promote group foraging? *Proceedings of the Royal Society London series B*. 270: 1137-1141.
- Shipley L.A., J.E. Gross, D.E. Spalinger, N.T. Hobbs and B.A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. *American Naturalist* 143: 1055-1082.
- Sjerps M. and P. Haccou. 1994. Effects of competition on optimal patch leaving: a war of attrition. *Theoretical Population Biology* 46: 300-318.
- Smith J.N.M. 1974. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. *Behaviour* 49: 1-61.
- Sokal R.R. and F.J. Rohlf. 1995. *Biometry*, third edition. W. H. Freeman and Co, New York.
- Sparrow A.D. 1999. A heterogeneity of heterogeneities. *Trends in Ecology and Evolution* 14: 422-423.
- Stahl J., P.H. Tolsma, M.J.J.E. Loonen and R.H. Drent. 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks *Animal Behaviour* 61: 257-264.
- Statsoft. 1999. *Statistica*, version 5.5, Tulsa, Oklahoma.
- Statsoft. 2004. *Statistica*, version 6.1, Tulsa, Oklahoma.
- Statsoft. 2005. *Statistica*, version 7.1, Tulsa, Oklahoma.
- Stephens D.W. 1989. Variance and the value of information. *American Naturalist* 134: 128-140.
- Stephens D.W. and J.R. Krebs. 1986. *Foraging theory*. Princeton University Press.
- Stewart A.J.A., E.A. John and M.J. Hutchings. 2000. The world is heterogeneous: ecological consequences of living in a patchy environment. *In*: M.J. Hutchings, E.A. John and A.J.A. Stewart (editors). *The ecological consequences of environmental heterogeneity*. Blackwell Science Ltd., Oxford. pp. 1-8.

- Stillman R.A., J.D. Goss-Custard and M.J. Alexander. 2000. Predator search pattern and the strength of interference through prey depression. *Behavioral Ecology* 11: 597-605.
- Stoll P. and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82: 319-327.
- Sutherland W.J. 1983. Aggregation and the 'ideal free' distribution. *Journal of Animal Ecology* 52: 821-828.
- Tenhumberg B., M.A. Keller, A.J. Tyre and H.P. Possingham. 2001. The effect of resource aggregation at different scales: Optimal foraging behavior of *Cotesia rubecula*. *American Naturalist* 158: 505-518.
- Thrush S.F. 1991. Spatial patterns in soft-bottom communities. *Trends in Ecology and Evolution* 6: 75-79.
- Tilman D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.
- Tinbergen J.M. 1981. Foraging decisions in starlings (*Sturnus vulgaris* L.). *Ardea* 69: 1-67.
- Turchin P. 1998. Quantitative analyses of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates Inc. Publishers, Sunderland.
- Tyler J.A. and W.W. Hargrove. 1997. Predicting spatial distribution of foragers over large resource landscapes: a modeling analysis of the Ideal Free Distribution. *Oikos* 79: 376-386.
- Vahl W.K., T. Lok, J. van der Meer, T. Piersma and F.J. Weissing. 2005. Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology* 16: 834-844.
- Valone T.J. 1989. Group foraging, public information, and patch estimation. *Oikos* 56: 357-363.
- Valone T.J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. *Animal Behaviour* 41: 569-577.
- Valone T.J. and J.S. Brown. 1989. Measuring patch assessment abilities of desert granivores. *Ecology* 70: 1800-1810.
- Valone T.J. and J.J. Templeton. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society London series B* 357: 1549-1557.
- van Eerden M.R. 1990. Waterfowl movements in relation to food stocks. *In*: J.D. Goss-Custard and W.G. Hale (editors). *Coastal waders and waterfowl in winter*. Cambridge University Press. pp. 84-100.
- van Eerden M.R., J.H. Beekman, M. Smit and K. Oosterbeek. 1997. Patch use by Bewick's Swans *Cygnus columbianus bewickii* feeding upon Sago Pondweed *Potamogeton pectinatus* in shallow lakes in the Netherlands: variation in exploitation threshold caused by social, environmental and time dependent factors. *In*: Van Eerden M.R. (editor). *Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands*. Rijkswaterstaat, Directie IJsselmeergebied, Lelystad, the Netherlands. pp. 111-132.
- van Gils J.A. 2004. General discussion: scaling up from physiological and behavioural ecology towards population-level processes. Box VI. Area-restricted search in a continuous environment. *In*: Foraging decisions in a digestively constrained long-distance migrant, the red knot (*Calidris canutus*). PhD Thesis, Groningen University, Groningen, The Netherlands.

- van Gils J.A., P. Edelaar, G. Escudero and T. Piersma. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for using more tools of behavioural ecology. *Oikos* 104: 197-204.
- van Gils J.A., I.W. Schenk, O. Bos and T. Piersma. 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *American Naturalist* 161: 777-793.
- van Gils J. A., B. Spaans, A. Dekinga and T. Piersma. 2006. Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology* 87: 1189-1202.
- van Wijk R.J. 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. *Aquatic Botany* 31: 211-258.
- Visser M.E. 1991. Prey selection by predators depleting a patch; an ESS model. *Netherlands Journal of Zoology* 41: 63-79.
- Walsh P.D. 1996. Area-restricted search and the scale dependence of patch quality discrimination. *Journal of Theoretical Biology* 183: 351-361.
- Wanink J. and L. Zwarts. 1985. Does an optimally foraging oystercatcher obey the functional response? *Oecologia* 67: 98-106.
- Wanink J.H. and L. Zwarts. 2001. Rate-maximizing optimality models predict when oystercatchers exploit a cohort of the bivalve *Scrobicularia plana* over a 7-year time span. *Journal of Animal Ecology* 70: 150-158.
- Ward J.F., R.M. Austin and D.W. Macdonald. 2000. A simulation model of foraging behaviour and the effect of predation risk. *Journal of Animal Ecology* 69: 16-30.
- Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385-397.
- Wiens J.A. 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. *In: M.J. Hutchings, E.A. John and A.J.A. Stewart (editors). The ecological consequences of environmental heterogeneity. Blackwell Science Ltd., Oxford. pp. 9-31.*
- Wilson S.L. and G.I.H. Kerley. 2003. Bite diameter selection by thicket browsers: the effect of body size and plant morphology on forage intake and quality. *Forest Ecology and Management* 181: 51-65.
- Zach R. and J.B. Falls. 1976. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. *Canadian Journal of Zoology* 54: 1863-1879.
- Zwarts L., A.-M. Blomert and J.H. Wanink. 1992. Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. *Marine Ecology Progress Series* 83 :129-139.
- Zwarts L., B.J. Ens, J.D. Goss-Custard, J.B. Hulscher and S.E.A. le V. dit Durell. 1996. Causes of variation in prey profitability and its consequences for the intake rate of the oystercatcher *Haematopus ostralegus*. *Ardea* 84A: 229-268.