

**Life-history responses, transmission dynamics and
epidemiology in a terrestrial gastropod infected with
parasitic mites**

Inauguraldissertation

zur Erlangung der Würde eines Doktors der Philosophie

vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

von
Hans Ulrich Schüpbach
aus Mirchel BE

Basel, 2010

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät der
Universität Basel auf Antrag von

Prof. Dr. Bruno Baur

Prof. Dr. Andreas Erhardt

Basel, den 10.11.2009

Prof. Dr. Eberhard Parlow

Dekan



Namensnennung-Keine kommerzielle Nutzung-Keine Bearbeitung 2.5 Schweiz

Sie dürfen:



das Werk vervielfältigen, verbreiten und öffentlich zugänglich machen

Zu den folgenden Bedingungen:



Namensnennung. Sie müssen den Namen des Autors/Rechteinhabers in der von ihm festgelegten Weise nennen (wodurch aber nicht der Eindruck entstehen darf, Sie oder die Nutzung des Werkes durch Sie würden entlohnt).



Keine kommerzielle Nutzung. Dieses Werk darf nicht für kommerzielle Zwecke verwendet werden.



Keine Bearbeitung. Dieses Werk darf nicht bearbeitet oder in anderer Weise verändert werden.

- Im Falle einer Verbreitung müssen Sie anderen die Lizenzbedingungen, unter welche dieses Werk fällt, mitteilen. Am Einfachsten ist es, einen Link auf diese Seite einzubinden.
- Jede der vorgenannten Bedingungen kann aufgehoben werden, sofern Sie die Einwilligung des Rechteinhabers dazu erhalten.
- Diese Lizenz lässt die Urheberpersönlichkeitsrechte unberührt.

Die gesetzlichen Schranken des Urheberrechts bleiben hiervon unberührt.

Die Commons Deed ist eine Zusammenfassung des Lizenzvertrags in allgemeinverständlicher Sprache: <http://creativecommons.org/licenses/by-nc-nd/2.5/ch/legalcode.de>

Haftungsausschluss:

Die Commons Deed ist kein Lizenzvertrag. Sie ist lediglich ein Referenztext, der den zugrundeliegenden Lizenzvertrag übersichtlich und in allgemeinverständlicher Sprache wiedergibt. Die Deed selbst entfaltet keine juristische Wirkung und erscheint im eigentlichen Lizenzvertrag nicht. Creative Commons ist keine Rechtsanwalts-gesellschaft und leistet keine Rechtsberatung. Die Weitergabe und Verlinkung des Commons Deeds führt zu keinem Mandatsverhältnis.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENT.....	5
SUMMARY.....	6
GENERAL INTRODUCTION.....	8
CHAPTER 1.....	17
Parasitic mites influence fitness components of their host, the land snail <i>Arianta arbustorum</i>	
CHAPTER 2.....	25
Within- and among-family variation in parasite load and parasite-induced mortality in the land snail <i>Arianta arbustorum</i> , a host of parasitic mites	
CHAPTER 3.....	36
Experimental evidence for a new transmission route in a parasitic mite and its mucus-dependent orientation towards the host snail	
CHAPTER 4.....	43
Contact-based transmission models in terrestrial gastropod populations infected with parasitic mites	
GENERAL DISCUSSION.....	66
CURRICULUM VITAE.....	74

ACKNOWLEDGEMENT

First of all I would like to thank Bruno Baur for the supervision, support, advice and collaboration throughout this thesis. I was particularly glad for his confidence and for the opportunity to work on a fascinating subject. Many thanks go to Andreas Erhardt for serving me as a co-referee of the thesis.

I would like to thank everyone who contributed to the thesis. I am grateful to all proofreaders of the manuscripts for their valuable input. Special thanks go to Annette Baur and her fascinating ability to detect faulty details in my manuscripts and to Joris Koene who made me aware what linguistic accuracy actually is. I am grateful to Nicole Minoretti and Kathleen Beese who introduced me in the field of snail care and the scientific methodology of the thesis. Many thanks go to all assistants who took over a significant part of the work in the lab. Without the help of Nadja Lang, Michael Coslovsky, Oliver Müller and Aurelia Wirth the accomplishment of the thesis would not have been possible.

Furthermore I like to thank all present and past members of the NLU who contributed to the convenient working conditions. Many thanks go to the people in room 21 and 24 for the scientific and non-scientific discussions. Further thanks go to the hermaphrodite groups in Tübingen and Antwerpen for organizing inspiring meetings and congresses.

For the non-scientific part of my thesis I want to thank my girlfriend Natalie Jaeger for the three fantastic years we spent together. Special thanks go to my family and friends for their support and their friendship throughout my PhD thesis.

Finally, I would like to thank Basel. It was a good place of work and a convenient residence during my PhD.

This thesis was funded by the Swiss National Science Foundation (grant 31-110061 to Bruno Baur).

SUMMARY

Parasites are known to influence the life-history of their hosts. A parasite-induced reduction in host fecundity and survival may lead to a reduced rate of increase in the host population. Genetic variation in parasite resistance and parasite-induced host mortality is a precondition for parasite-induced selection on host populations and enables parasites to influence their host's population genetics. The occurrence and the distribution of parasites in host populations are determined by parasite transmission. Transmission among host individuals is one of the most important characteristics in the life cycle of a parasite species, and is fundamentally important for the parasite's fitness. Parasite-induced life-history responses and the dynamics of parasite transmission are key elements of the epidemiology. Mathematical models of parasite transmission and the host life-history may help to understand the dynamics of host- and parasite populations and are essential to predict the course of infectious diseases, which are especially important in the context of veterinary and human health care.

In the present thesis we investigated the impact of *Riccardoella limacum*, a parasitic mite of terrestrial gastropods, on life-history of *Arianta arbustorum*, a common host of *R. limacum*. Furthermore, we examined the transmission dynamics of *R. limacum*. Data on parasite-induced life-history responses in *A. arbustorum* and on parasite transmission were then combined in mathematical models, in order to predict the epidemiology and to assess disease relevant parameters, which may help to predict the course of *R. limacum* infections in *A. arbustorum* populations.

In order to assess the impact of *R. limacum* on the life-history of *A. arbustorum*, we quantified the reproductive output (number of eggs), the hatching success of the eggs and the activity of naturally infected snails. The reproductive output was reduced in infected snails, whereas the hatching success of the eggs was slightly increased in infected snails compared to parasite-free snails. Snail behavior differed between infected and parasite-free snails by a reduced activity of parasite infected snails. Furthermore, in 2 out of 3 *A.*

arbustorum populations and in experimentally infected snails winter survival was reduced in infected snails compared to uninfected snails.

In order to quantify the additive genetic variation in parasite load and winter mortality, every second snail of 15 lab bred snail families was experimentally infected with *R. limacum*. Parasite load of infected snails showed high heritable variation among snail families, suggesting additive genetic variation in parasite resistance in *A. arbustorum*. Furthermore, parasite load increased with increasing snail size within snail family, which suggests that the proliferation of *R. limacum* is limited by resources provided by *A. arbustorum*.

Furthermore, the transmission route of *R. limacum* was investigated. Parasite transmission also occurred without physical contact from mite-infected to parasite-free snails. The investigation of the off-host locomotion of *R. limacum* revealed that mites prefer to move on fresh mucus. Apart from the transmission during long-lasting courtship and mating of the host, *R. limacum* is also transmitted via soil and may use fresh snail mucus a cue to locate new host.

Further transmission experiments revealed that transmission of *R. limacum* occurs for the most part during host contacts. Using experimentally assessed transmission probabilities per host contact and contact frequencies of *A. arbustorum*, we developed mathematical models based on contact frequencies and transmission probabilities of *A. arbustorum*. Data on parasite-induced life-history responses were used to assess the basic reproductive ratio (R_0 ; expected number of secondary infections originated by an infected individual introduced into a susceptible population) and host threshold density for parasite persistence in three *A. arbustorum* populations. The models revealed that the population with the highest density showed larger R_0 -values (16.7–22.95) compared to populations with intermediate (2.72–7.45) or low population density (0.75–4.10). Host threshold population density for parasite persistence ranged from 0.35 to 2.72 snails per m². The thesis shows that the incorporation of the disease-relevant biology of organisms may improve models of host-parasite dynamics. This approach may help to predict the epidemiology of host-parasite systems.

GENERAL INTRODUCTION

Parasites are known to influence life-history traits and the behavior of their hosts (e.g., Minchella and Scott, 1991; Agnew et al., 2000). Parasite infection may induce both short-term physiological and evolutionary responses (Koella and Restif, 2001; Krist, 2006). A prerequisite for an impact at the population level is a parasite-induced increase in mortality and/or a decrease in fecundity of the host, leading to a reduced mean rate of increase in the host population (Jaenike et al., 1995). As a result of co-evolutionary processes, reduced individual fecundity and survival may lead to an increase in the reproductive effort (Forbes, 1993; Perrin et al., 1996; Gandon et al., 2002) and favor early reproduction in host populations (Hochberg et al., 1992; Restif et al., 2001). However, the impact of parasite pressure on host populations strongly depends on the environmental conditions (Jokela et al., 2005; Mitchell et al., 2005) and on the attributes of the parasite (Forbes, 1993; Day, 2001).

Hosts individuals differ in their susceptibility to parasite infection. Additive genetic variation in host resistance against parasite infection is a key assumption in models of host-parasite coevolution (Mitchell et al., 2005; Little et al., 2006). Variation in host susceptibility (Grenfell et al., 2004) and in parasite-induced effects on host survival and fertility (Jaenike et al., 1995) may influence the epidemiology of host-parasite systems (Agnew et al., 2000). Mechanisms enabling vertebrate hosts to resist against ectoparasite infection have received considerable attention (e.g. Christe et al., 2000; Wikel and Alarcon-Chaidez, 2001; Roulin et al., 2007). The plasticity of their adaptive immune system promotes a high variability in the genetic background, allowing hosts to cope with parasite infection (Lazzaro and Little, 2009). In invertebrate hosts, the genetic background of resistance against ectoparasites is much less studied (Wikel and Alarcon-Chaidez, 2001). Knowledge on heritability in parasite resistance mainly originates from insect hosts (Polak, 2003; Luong et al., 2007). However, in other taxa such as terrestrial gastropods, the heritability of resistance against ectoparasites is poorly understood.

Parasitism is known to play an important role in the ecology and evolution of natural freshwater snail populations, for example in the evolution of life-history and sexual

reproduction (Jokela and Lively, 1995; Lively, 1996; Dillon, 2000), host resistance (Webster and Woolhouse, 1999) and host-parasite co-evolution (Dybdahl and Lively, 1998). However, the impact of ectoparasite infection on the terrestrial gastropod populations is poorly understood. Several terrestrial gastropods are infected by *Riccardoella limacum* (SCHRANK 1776), a parasitic mite that lives in the mantle cavity of their host (Turk and Phillips, 1946; Fain and van Goethem, 1986; Baur and Baur, 2005). The parasite's life cycle has been studied under laboratory conditions in the host snail *Cornu aspersum* (Graham, 1994). Female mites lay the eggs in the lung tissue of their host. Three nymphal mite stages are followed by sexually mature males and females, both 0.4mm in body length (Baker, 1970a). The total life cycle in *R. limacum* lasts 19–23 d at temperatures of 20°–25°C. During hibernation of the host, adult mites rarely survive in the lung, but a new generation of larvae emerges from overwintered eggs in the pulmonary cavity in spring. *Riccardoella limacum* is a blood-sucking parasite (Baker, 1970b). A strong impact of the parasite on host growth and reproductive development has been shown in *Cornu aspersum* (MÜLLER 1774) under laboratory conditions (Graham, 1994; Graham et al., 1996). These adverse effects can seriously influence the economy of commercial snail farming. However, little is known about the parasite's influence on host life-history, behavior, and dynamics of natural snail populations. In *Arianta arbustorum* (LINNAEUS 1758), a considerable variation in the prevalence and intensity of *R. limacum* infection was found in wild populations in Switzerland (Baur and Baur, 2005). The parasite occurred in four out of 11 populations examined with a prevalence of 45.8–77.8%.

Parasite transmission in a host population is a fundamental component of the parasite's fitness (Fenton et al., 2002; Galvani, 2003), and is closely linked to other traits such as fecundity, survival and virulence (Bull, 1994; Ebert and Herre, 1996; Crossan et al., 2007). Furthermore, the transmission route of parasites affects the distribution of the parasite in the host population and is an important factor in the epidemiology of host-parasite systems (Fenton et al., 2002). In macroparasites, the transmission among hosts is often actively occurring during host contact or through mobile, free-living stages of the parasite (Combes, 2001). Since suitable hosts are patchily distributed in space and time,

the optimal strategy for transmission depends on both the mechanisms of parasite transmission (Fenton and Rands, 2004; Robb and Forbes, 2005) and on the spatial structure of the host population (Boots and Meador, 2007; Crossan et al., 2007). Strong selection pressure on parasites to develop optimal strategies to maximize their likelihood of successful transmission may therefore be expected (Fenton and Rands, 2004; Poulin, 2007). A possible strategy to increase the probability of transmission and to locate new hosts is the use of signals from the environment or from the host (Rea and Irwin, 1994; Krasnov et al. 2002; Hertel et al. 2006). *Riccardoella limacum* is actively transmitted during courtship and mating of the host *A. arbustorum*. Mites leave the mantle cavity, move over the soft body of the snail, and switch to the new host. However, mites have also been observed in juvenile snails (Baur and Baur, 2005), suggesting other ways of parasite transmission. Snails secrete mucus during locomotion. The adhesive and lubricant characteristics of mucus permit adhesion to the substrate and snail locomotion (Barker, 2001). Mucus is also important for the communication among snails. Mucus trails could be used by *R. limacum* to find new hosts.

Attributes of the transmission process strongly differ both among hosts and among parasites. The population density of hosts (Greer et al., 2008), contact rate among hosts (Balenghien et al., 2005) and host behavior (Ryder et al., 2007; Greer and Collins, 2008) as well as the mode of transmission (Clayton and Tompkins, 1994), the dose of transmitted parasites (Ben-Ami et al., 2008) and their infectivity (Bull, 1994) may lead to pronounced differences in the epidemiology of the interacting species (Fenton et al., 2002; Ganusov and Antia, 2003; Frank and Schmid-Hempel, 2008). In epidemiological models, parasite transmission is generally expressed by the transmission coefficient (β), which specifies the rate at which parasites are transmitted among infected and susceptible hosts. Since transmission coefficients are highly disease-specific, the decomposition of the transmission term into disease-specific aspects of the transmission process may enhance the accuracy and strongly increase the quality of epidemiological models (Begon et al., 2002; Real and Biek, 2007; Antolin, 2008; Alizon et al., 2009). Furthermore, this approach may improve the assessment of important disease-specific terms including the basic reproductive ratio (R_0), which is defined as the expected number of secondary

infections originated by an infected individual introduced into a susceptible population (Heesterbeek, 2002; Antia et al., 2003).

FOCUS OF THE THESIS

The focus of this thesis was to quantify the impact of *R. limacum* on life-history and behavior of *A. arbustorum* and to examine transmission dynamics of *R. limacum* among host individuals. We combined the findings on life-history and parasite transmission and formulated epidemiological transmission models in order to predict the dynamics of *R. limacum* in *A. arbustorum* populations.

In **CHAPTER 1** we assessed the impact of *R. limacum* infection on female reproductive output (egg number), hatching success of eggs and the behavior in naturally infected *A. arbustorum* individuals. Furthermore, we quantified the mortality during hibernation in three naturally infected snail populations and in experimentally infected snails. In **CHAPTER 2** we infected every second snail of 15 snail families in order to investigate the genetic background of among- and within-family variation in parasite load and winter mortality of experimentally infected snail families. In **CHAPTER 3** we investigated the transmission route of *R. limacum* and examined the off-host locomotion of mites, which enables the parasite to locate new hosts. In **CHAPTER 4** we explored the influence of host contact rate, parasite intensity and host behavior on the transmission success of *R. limacum*, and we calculated the probability of parasite transmission during host encounters. Using these results we developed epidemiological models based on host contact frequencies and transmission probabilities during host encounters. We parameterized the models with data on three snail populations in order to predict the dynamics of *R. limacum* in *A. arbustorum* populations.

REFERENCES

Agnew, P., Koella, J.C. and Michalakis, Y. (2000) Host life history responses to parasitism. *Microbes Infect.* 2, 891-896.

- Alizon, S., Hurford, N., Mideo, N. and Van Baalen, M. (2009) Virulence evolution and the trade-off hypothesis: history, current state of affairs and the future. *J. Evol. Biol.* 22, 245-259.
- Antia, R., Regoes, R.R., Koella, J.C. and Bergstrom, C.T. (2003) The role of evolution in the emergence of infectious diseases. *Nature* 426, 658-661.
- Antolin, M.F. (2008) Unpacking beta: within-host dynamics and the evolutionary ecology of pathogen transmission. *Annu. Rev. Ecol Evol. Syst.* 39, 415-437.
- Baker, R.A. (1970a) Studies on the life history of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes). *J. Nat. Hist.* 4, 511-519.
- Baker, R.A. (1970b) The food of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes) and its relationship with pulmonate molluscs. *J. Nat. Hist.* 4, 521-530.
- Balenghien, T., Chalvet-Monfray, K., Bicout, D.J. and Sabatier, P. (2005) Modelling and determination of the transmission contact rate for contagious bovine pleuropneumonia. *Epidemiol. Infect.* 133, 337-342.
- Barker, G.M. (2001) The biology of terrestrial molluscs. In, CABI Publishing, Wallingsford, Oxon.
- Baur, A. and Baur, B. (2005) Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebr. Biol.* 124, 194-201.
- Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M. and Turner, J. (2002) A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiol. Infect.* 129, 147-153.
- Ben-Ami, F., Regoes, R.R. and Ebert, D. (2008) A quantitative test of the relationship between parasite dose and infection probability across different host-parasite combinations. *Proc. R. Soc. B* 275, 853-859.
- Boots, M. and Meador, M. (2007) Local interactions select for lower pathogen infectivity. *Science* 315, 1284-1286.
- Bull, J.J. (1994) Virulence. *Evolution* 48, 1423-1437.

- Christe, P., Arlettaz, R. and Vogel, P. (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). *Ecol. Letters* 3, 207-212.
- Clayton, D.H. and Tompkins, D.M. (1994) Ectoparasite virulence is linked to mode of transmission. *Proc. R. Soc. B* 256, 211-217.
- Combes, C. (2001) *Parasitism: The ecology and evolution of intimate interactions*. The University of Chicago Press, Chicago.
- Crossan, J., Paterson, S. and Fenton, A. (2007) Host availability and the evolution of parasite life-history strategies. *Evolution* 61, 675-684.
- Dillon, R.T. (2000) *The ecology of freshwater molluscs*. Cambridge University Press, Cambridge.
- Day, T. (2001) Parasite transmission modes and the evolution of virulence. *Evolution* 55, 2389-2400.
- Dybdahl, M.F., Lively, C.M. (1998) Host-parasite coevolution: Evidence for rare advantage and time-lagged selection in a natural population. *Evolution* 52, 1057-1066.
- Ebert, D. and Herre, E.A. (1996) The evolution of parasitic diseases. *Parasitol. Today* 12, 96-101.
- Fain, A. and van Goethem, J.L. (1986) Les acariens du genre *Riccardoella* Berlese, 1923 parasites du poumon de mollusques gastéropodes pulmonés terrestres. *Acarologia* 27, 125-140.
- Fenton, A., Fairbairn, J.P., Norman, R. and Hudson, P.J. (2002) Parasite transmission: reconciling theory and reality. *J. Anim. Ecol.* 71, 893-905.
- Fenton, A. and Rands, S.A. (2004) Optimal parasite infection strategies: a state-dependent approach. *Int. J. Parasitol.* 34, 813-821.
- Forbes, M.R.L. (1993) Parasitism and host reproductive effort. *Oikos* 67, 444-450.
- Frank, S.A. and Schmid-Hempel, P. (2008) Mechanisms of pathogenesis and the evolution of parasite virulence. *J. Evol. Biol.* 21, 396-404.
- Galvani, A.P. (2003) Epidemiology meets evolutionary ecology. *Trends Ecol. Evol.* 18, 132-139.

- Gandon, S., Agnew, P. and Michalakis, Y. (2002) Coevolution between parasite virulence and host life-history traits. *Am. Nat.* 160, 374-388.
- Ganusov, V.V. and Antia, R. (2003) Trade-offs and the evolution of virulence of microparasites: do details matter? *Theor. Popul. Biol.* 64, 211-220.
- Graham, F. (1994) The biology and control of *Riccardoella limacum* (Schrank), a mite pest of farmed snails. PhD dissertation, University of Wales.
- Graham, F.J., Runham, N.W. and Ford, J.B. (1996) Long-term effects of *Riccardoella limacum* living in the lung of *Helix aspersa*. *BCPC Symposium Proceedings* 66, 359-364.
- Greer, A.L., Briggs, C.J. and Collins, J.P. (2008) Testing a key assumption of host-pathogen theory: density and disease transmission. *Oikos* 117, 1667-1673.
- Greer, A.L. and Collins, J.P. (2008) Habitat fragmentation as a result of biotic and abiotic factors controls pathogen transmission throughout a host population. *J. Anim. Ecol.* 77, 364-369.
- Grenfell, B.T., Pybus, O.G., Gog, J.R., Wood, J.L.N., Daly, J.M., Mumford, J.A. and Holmes, E.C. (2004) Unifying the epidemiological and evolutionary dynamics of pathogens. *Science* 303, 327-332.
- Heesterbeek, J.A.P. (2002) A brief history of R_0 and a recipe for its calculation. *Acta Biotheor.* 50, 189-204.
- Hertel, J., Holweg, A., Haberl, B., Kalbe, M. and Haas, W. (2006) Snail odour-clouds: spreading and contribution to the transmission success of *Trichobilharzia ocellata* (Trematoda, Digenea) miracidia. *Oecologia* 147, 173-180.
- Hochberg, M.E., Michalakis, Y. and de Meeus, T. (1992) Parasitism as a constraint on the rate of life-history evolution. *J. Evol. Biol.* 5, 491-504.
- Jaenike, J., Benway, H. and Stevens, G. (1995) Parasite-induced mortality in mycophagous *Drosophila*. *Ecology* 76, 383-391.
- Jokela, J. and Lively, C.M. (1995) Parasites, sex, and early reproduction in a mixed population of freshwater snails. *Evolution* 49, 1268-1271.

- Jokela, J., Taskinen, J., Mutikainen, P. and Kopp, K. (2005) Virulence of parasites in hosts under environmental stress: experiments with anoxia and starvation. *Oikos* 108, 156-164.
- Koella, J.C. and Restif, O. (2001) Coevolution of parasite virulence and host life history. *Ecol. Letters* 4, 207-214.
- Krasnov, B.R., Khokhlova, I.S., Oguzoglu, I. and Burdelova, N.V. (2002) Host discrimination by two desert fleas using an odour cue. *Anim. Behav.* 64, 33-40.
- Krist, A.C. (2006) Prevalence of parasites does not predict age at first reproduction or reproductive output in the freshwater snail, *Helisoma anceps*. *Evol. Ecol. Res.* 8, 753-763.
- Little, T.J., Watt, K. and Ebert, D. (2006) Parasite-host specificity: Experimental studies on the basis of parasite adaptation. *Evolution* 60, 31-38.
- Lively, C.M. (1996) Host-parasite coevolution and sex: do interactions between biological enemies maintain genetic variation and cross-fertilization? *BioScience* 46, 107-114.
- Luong, L.T., Heath, B.D. and Polak, M. (2007) Host inbreeding increases susceptibility to ectoparasitism. *J. Evol. Biol.* 20, 79-86.
- Minchella, D.J. and Scott, M.E. (1991) Parasitism – a cryptic determinant of animal community structure. *Trends Ecol. Evol.* 6, 250-254.
- Mitchell, S.E. and Read, A.F. (2005) Poor maternal environment enhances offspring disease resistance in an invertebrate. *Proc. R. Soc. B* 272, 2601-2607.
- Mitchell, S.E., Rogers, E.S., Little, T.J. and Read, A.F. (2005) Host-parasite and genotype-by-environment interactions: Temperature modifies potential for selection by a sterilizing pathogen. *Evolution* 59, 70-80.
- Perrin, N., Christe, P. and Richner, H. (1996) On host life-history response to parasitism. *Oikos* 75, 317-320.
- Polak, M. (1996) Ectoparasitic effects on host survival and reproduction: the *Drosophila-Macrocheles* association. *Ecology* 77, 1379-1389.
- Poulin, R. (2007) *Evolutionary ecology of parasites*. Princeton University Press, Princeton.

- Rea, J.G. and Irwin, S.W.B. (1994) The ecology of host-finding behavior and parasite transmission - past and future perspectives. *Parasitology* 109, S31-S39.
- Real, L.A. and Biek, R. (2007) Infectious disease modeling and the dynamics of transmission. *Wildlife and emerging zoonotic diseases: the biology, circumstances and consequences of cross-species transmission. Curr. Topics Microbiol. Immunol.* 315, 33-49.
- Restif, O., Hochberg, M.E. and Koella, J.C. (2001) Virulence and age at reproduction: new insights into host-parasite coevolution. *J. Evol. Biol.* 14, 967-979.
- Robb, T. and Forbes, M.R. (2005) Success of ectoparasites: how important is timing of host contact? *Biol. Letters* 1, 118-120.
- Ryder, J.J., Hathway, J. and Knell, R.J. (2007) Constraints on parasite fecundity and transmission in an insect-STD system. *Oikos* 116, 578-584.
- Turk, F.A. and Phillips, S.M. (1946) A monograph of the slug mite - *Riccardoella limacum* (Schrank). *Proc. Zool. Soc. Lond.* 115, 448-472.
- Webster, J.P. and Woolhouse, M.E.J. (1999) Cost of resistance: relationship between reduced fertility and increased resistance in a snail-schistosome host-parasite system. *Proc. R. Soc. B* 266, 391-396.
- Wikel, S.K. and Alarcon-Chaidez, F.J. (2001) Progress toward molecular characterization of ectoparasite modulation of host immunity. *Vet. Parasitol.* 101, 275-287.

CHAPTER 1

Parasitic mites influence fitness components of their host, the
land snail *Arianta arbustorum*

Hans Ulrich Schüpbach and Bruno Baur

Invertebrate Biology (2008) 127: 350–356

Parasitic mites influence fitness components of their host, the land snail *Arianta arbustorum*

Hans U. Schüpbach^a and Bruno Baur

Department of Environmental Sciences, Section of Conservation Biology, University of Basel, Basel, Switzerland

Abstract. Parasites can influence the population dynamics of their hosts by affecting life-history strategies and behavior. The hematophagous mite *Riccardoella limacum* lives in the lung cavity of terrestrial gastropods. We used correlational and experimental approaches to investigate the influence of parasite infection on the behavior and life-history traits of the simultaneously hermaphroditic land snail *Arianta arbustorum*, a common host of *R. limacum*. Naturally infected individuals of *A. arbustorum*, collected in the wild, showed a decreased activity compared with uninfected snails. The reproductive output, expressed as the number of eggs deposited in a reproductive season, was reduced in mite-infected hosts. However, the hatching success of the eggs laid by parasitized snails was slightly higher than that of uninfected individuals. We also examined winter survival in 361 adults of *A. arbustorum* collected from four natural populations. The prevalence of mite infection ranged from 44.8% to 70.1% in three populations (snails in the fourth population were not infected). Winter survival was reduced in infected snails in two out of three populations. Furthermore, experimentally infected snails from an uninfected population showed a reduced winter survival compared with control snails. Our results indicate that parasite pressure imposed by members of *R. limacum* may influence life history in *A. arbustorum*.

Additional key words: terrestrial gastropod, reproduction, survival, life history

Parasites are known to influence life history traits and the behavior of their hosts (e.g., Minchella & Scott 1991; Agnew et al. 2000). Parasite infection may induce both short-term physiological and evolutionary responses (Koella & Restif 2001; Krist 2006). A prerequisite for an impact at the population level is a parasite-induced increase in mortality and/or a decrease in fecundity of the host, leading to a reduced mean rate of increase in the host population (Jaenike et al. 1995). As a result of co-evolutionary processes, reduced individual fecundity and survival may lead to an increase in the reproductive effort (Forbes 1993; Perrin et al. 1996; Gandon et al. 2002) and favor early reproduction in host populations (Hochberg et al. 1992; Restif et al. 2001). However, the effect of parasite pressure on host populations strongly depends on the environmental conditions (Jokela et al. 2005; Mitchell et al. 2005) and on the attributes of the parasite (Forbes 1993; Day 2001). Besides fecundity and mortality, parasites can manipulate their host's

behavior (De Jong-Brink & Koene 2005). Parasites frequently influence the activity and locomotion of their hosts, which may result in reduced dispersal, reduced foraging ability, and decreased predator avoidance ability (Goater et al. 1993). A reduced activity in turn can lead to a decreased growth rate. For example, the activity of the helioid snail *Cepaea nemoralis* LINNAEUS 1758 was positively correlated with the relative growth rate both under field and under laboratory conditions (Oosterhoff 1977).

Several pulmonate terrestrial gastropods are infected by members of *Riccardoella limacum* SCHRANK 1776, a parasitic mite that lives in the lung of their hosts (Turk & Phillips 1946; Baker 1970a,b; Fain & van Goethem 1986; Baur & Baur 2005). A strong impact by the parasite on host growth and reproductive development has been shown in *Cornu aspersum* MÜLLER 1774 (formerly *Helix aspersa*) under laboratory conditions (Graham 1994; Graham et al. 1996). These adverse effects can seriously influence the economy of commercial snail farming. However, little is known about the parasite's influence on host life history, behavior, and dynamics of natural populations.

^a Author for correspondence.

E-mail: H.Schuepbach@unibas.ch

In the present study, we used correlative and experimental approaches to investigate life-history consequences of members of *R. limacum* on those of the host *Arianta arbustorum* LINNAEUS 1758, a simultaneously hermaphroditic land snail. Individuals of *R. limacum* frequently occur in this snail, and show a high inter-population variation in the prevalence and intensity of infection (Baur & Baur 2005).

The aim of our study was to investigate associations between parasite infection and relevant life-history traits in *A. arbustorum*. We used naturally infected adults of *A. arbustorum* from wild populations to examine the relationship between parasite infection and snail activity, current reproductive output, and winter survival in *A. arbustorum*. We also experimentally infected snails from an uninfected wild population to examine the effect of parasitic mites on the host's winter survival. In particular, we addressed the following questions: (1) Is the parasite infection correlated with activity in *A. arbustorum*? (2) Is the infection by *R. limacum* associated with a reduced egg production and a reduced hatching success of the host? (3) Do individuals infected by *R. limacum* suffer a higher mortality during hibernation?

Methods

Study organisms

Members of *Arianta arbustorum* are simultaneously hermaphroditic helicid land snails, common in moist habitats of northwestern and central Europe (Kerney & Cameron 1979). The snail has determinate growth (shell breadth of adults 16–24 mm). Individuals become sexually mature at an age of 2–4 years and live for another 3–4 years (maximum 14 years; Baur & Raboud 1988). In the field, snails deposit one to three clutches, each consisting of 20–80 eggs, per reproductive season (Baur 1988, 1990). Individuals usually reproduce through outcrossing, but self-fertilization may occur after being isolated for 2–3 years (Chen 1994).

Riccardoella limacum is a parasitic mite that lives in the pulmonary cavity of helicid land snails (Fain & van Goethem 1986). The parasite's life cycle has been studied under laboratory conditions in the host snail *Cornu aspersum* (Graham 1994). Female mites lay the eggs in the lung tissue of their host. Three nymphal mite stages are followed by sexually mature males and females, both 0.4 mm in body length (Baker 1970a). The total life cycle in *R. limacum* lasts 19–23 d at temperatures of 20°–25°C. During hibernation of the host, adult mites rarely survive in the lung,

but a new generation of larvae emerges from overwintered eggs in the pulmonary cavity in spring. Members of *R. limacum* are blood-sucking parasites (Baker 1970b) that cause considerable harm in *C. aspersum* by reducing the activity and the growth rate, and by delaying reproductive development (Graham et al. 1996). A considerable variation in the prevalence and intensity of infection by *R. limacum* was found in wild populations of *A. arbustorum* in Switzerland (Baur & Baur 2005). The parasite occurred in four out of 11 populations examined with a prevalence of 45.8–77.8%. The intensity of mite infection was the highest in fall.

Activity and female reproductive output

Individuals of *A. arbustorum* were collected in Arlesheim, 7 km SE of Basel, Switzerland (47°30'N, 7°38'E), in the embankment of a track at a forest edge at an elevation of 380 m a.s.l., early in spring. Snails were transported to the laboratory and kept singly in transparent plastic beakers (6.5 cm in diameter, 8 cm deep) on moist soil mixed with powdered limestone under a light:dark regime of 16:8 h and a constant temperature of 19°C ± 1°C. The beakers were cleaned one to two times per week and fresh lettuce was provided *ad libitum* as food.

To assess the prevalence and intensity of parasite infection, we used a non-invasive screening method (Baur & Baur 2005). The soft body and respiratory pore of each individual were carefully examined for mites using a magnifying glass (×10). Mite screening was repeated three times on different days. Parasite screening was only performed when snails were active (extended soft body). The intensity of infection was expressed as the mean number of mites observed in the three examinations. The actual number of mites found in the lung of dissected host snails was about 10 × higher in fall than the mite intensity estimated with the non-invasive screening method before the dissection (Baur & Baur 2005).

The activity of snails was assessed 13 × over a period of 6 weeks. We classified the activity of each snail using a five-grade scale (0 = no activity, soft body retracted and shell aperture closed with an epiphragm; 1 = soft body retracted; 2 = soft body extended but tentacles retracted; 3 = soft body and tentacles extended; 4 = snail crawling or feeding). The overall activity of a snail was expressed as the cumulative percentage of records of an individual in the activity classes 2, 3, and 4.

To examine the association between parasite load and the female reproductive output of single snails, the eggs deposited were collected over a period of 10

weeks. The eggs of each clutch were cleaned on a moist paper towel and counted. A sub-sample of each batch ($67.1 \pm 2.8\%$ of all eggs; mean \pm SE) was incubated at $19^\circ\text{C} \pm 1^\circ\text{C}$ to record the hatching success of the eggs. Hatching success was expressed as the mean percentage of all eggs that hatched calculated for all batches of each individual snail.

We measured the shell breadth and height of each snail to the nearest 0.1 mm using a vernier caliper and calculated shell volume using the formula: shell volume = $0.312 \times [(\text{shell breadth})^2 \times \text{shell height}] - 0.038$ (B. Baur, unpubl. data). Shell volume is a more reliable measurement of snail size than mass, because mass depends on the state of hydration and thus is highly variable in terrestrial gastropods.

Winter survival

To examine the relationship between parasite infection and winter survival, we collected adult individuals of *A. arbustorum* at four localities in Switzerland in autumn (referred to, for convenience, as populations): Weissenstein ($47^\circ 15.0' \text{N}$, $7^\circ 28.5' \text{E}$; elevation 1230 m), Thun ($46^\circ 44' \text{N}$, $7^\circ 35' \text{E}$; 580 m), Nuglar ($47^\circ 29' \text{N}$, $7^\circ 42' \text{E}$; 430 m), and Allschwil ($47^\circ 32' \text{N}$, $7^\circ 31' \text{E}$; 335 m). Snails were transported to the laboratory, kept singly in transparent plastic beakers, and screened for the prevalence and intensity of *R. limacum* infection as described above. After 2 weeks, the snails were allowed to hibernate at 4°C and darkness in beakers lined with 4 cm moist soil (no food was provided). These conditions are similar to those of hibernating snails buried in soil in the field (Baur 1994). Hibernating snails were checked every second week to record dead animals. Hibernation lasted 24 weeks, as found in natural sub-alpine populations (Baur 1986). After this period, the snails were aroused by resetting the temperature, light regime, and food supply to the conditions before hibernation. We recorded dead animals for another 3 weeks after the snails emerged from hibernation.

Winter survival of infected snails

Seventy-five sub-adult individuals were collected in a parasite-free sub-alpine population near Gurnigelbad, 30 km south of Bern, Switzerland ($46^\circ 45' \text{N}$, $7^\circ 27' \text{E}$; elevation 1330 m), on July 29, 2006. Snails were kept under conditions as described above. The snails attained sexual maturity within 6 weeks, as indicated by the formation of a reflected shell lip. Between September 5 and 14, 2006, 41 randomly chosen snails (54.7%) were experimentally infected with members of *R. limacum*. Mites were obtained

from parasite-infected individuals of *A. arbustorum* collected in the Nuglar population. With a small, moistened paintbrush, six adult mites were transferred to the soft body of an uninfected snail. We waited until the transmitted mites entered the pulmonary cavity before placing the infected snails back into their beaker. Transmitted mites were allowed to reproduce for 6 weeks on their host (two mite generations; Graham et al. 1996). Afterwards, the snails were allowed to hibernate for 24 weeks as described above. The remaining 31 snails served as uninfected control and were allowed to hibernate at the same time under identical conditions. The mite intensity of experimentally infected snails is in the range of mite intensities observed in natural populations (Baur & Baur 2005; H.U. Schüpbach, unpubl. data).

Statistical analysis

Data analysis was performed using R Statistical Software (R Development Core Team 2006). We used linear regression to examine the relationships between parasite intensity, snail activity, and reproductive success. Percentage data were arcsine transformed and the numbers of eggs were log transformed. Pearson's correlations were calculated for correlations among reproductive traits. For the survival analyses, we used Cox's proportional hazard regression models. Means \pm SE are reported.

Results

Activity

Twenty-nine of the 53 adults of *Arianta arbustorum* (54.7%) collected in Arlesheim were infected with members of *Riccardoella limacum*. The intensity of infection ranged 0–6 mites. The mean intensity among infected individuals was 1.9 ± 0.3 mites ($n = 29$). Parasite intensity was not influenced by snail size ($F_{1,51} = 1.12$, $p = 0.294$).

We recorded the activity of 53 individuals $13 \times$ during the daytime. In 22.9% of the cases, the soft body was retracted and the shell aperture closed with an epiphragm, and in a further 44.1% the soft body was retracted. Snails were active in 33.0% of the cases. In 14.7% of the cases, the snails had the soft body extended but their tentacles retracted (activity class 2), in 11.5% of the cases the soft body and tentacles extended (activity class 3), and in 6.8% of the cases the snails were crawling or feeding (activity class 4).

At the individual level, the overall activity of a snail was negatively related to the intensity of

Table 1. Parasite prevalence, mean parasite intensity of infected individuals, and winter survival of individuals of *Arianta arbustorum* infected by individuals of *Riccardoella limacum* in four populations. *n* = number of snails examined.

Population	Parasite prevalence		Parasite intensity			Winter survival (%)
	% infection	<i>n</i>	Mean ± SE	Range	<i>n</i>	
Weissenstein	44.8	105	0.50 ± 0.04	0.3–1.3	47	69.5
Thun	70.1	77	1.72 ± 0.24	0.3–7.3	54	66.2
Nuglar	60.0	105	1.14 ± 0.12	0.3–5.0	63	90.5
Allschwil	0	74	—	—	—	86.5

parasite infection ($F_{1,51} = 5.84$, $p = 0.019$), while the overall activity of a snail was not related to shell size ($F_{1,51} = 1.56$, $p = 0.217$).

Female reproductive output

Snails laid an average of 130.8 ± 7.9 eggs during the study, deposited in 2.5 ± 0.2 batches, with a mean clutch size of 56.0 ± 2.3 eggs. The mean clutch size increased with shell size (Pearson's correlation: $r = 0.38$, $n = 49$, $p = 0.007$), whereas the number of batches deposited decreased with shell size ($r = -0.41$, $n = 49$, $p = 0.004$). Thus, the mean clutch size was negatively correlated with the number of batches laid ($r = -0.44$, $n = 49$, $p = 0.002$). The total number of eggs deposited, however, was not influenced by shell size ($F_{1,47} = 2.95$, $p = 0.092$). Considering mite infection, adults of *A. arbustorum* produced fewer total eggs with increasing parasite intensity ($F_{1,47} = 4.88$, $p = 0.032$).

The hatching success of eggs averaged $80.8 \pm 2.8\%$. The mean hatching success of eggs of

a snail was not affected by its shell size ($F_{1,47} = 0.33$, $p = 0.569$). However, the hatching success of eggs was slightly higher in snails with increased intensity of mite infection ($F_{1,47} = 5.71$, $p = 0.021$).

Winter survival

In total, we collected 361 individuals of *A. arbustorum*. In the Allschwil population, all snails collected were parasite-free, whereas in the Weissenstein, Thun, and Nuglar populations the mean prevalence of *R. limacum* was 57.1%. Among the infected individuals from all populations, the mean intensity of the infection was 1.1 ± 0.1 mites. However, there was a considerable variation in the prevalence and intensity of infection and in winter survival among the four populations of *A. arbustorum* (Table 1).

Overall, 78.4% of the hibernating snails survived the winter. However, the four populations differed in winter survival (Fig. 1). Among the three parasite-infected populations, winter survival was negatively

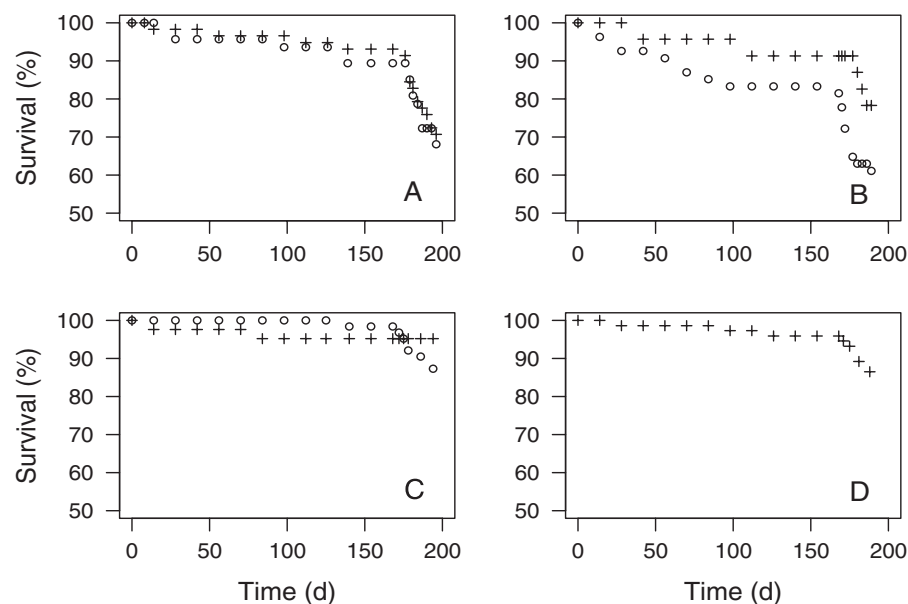


Fig. 1. Survivorship curves of infected (○) and uninfected (+) individuals of *Arianta arbustorum* from four populations, hibernating at 4°C: (A) Weissenstein, (B) Thun, (C) Nuglar, and (D) Allschwil.

related to parasite intensity (Likelihood ratio test = 21.8, $n = 287$, $p < 0.001$). Considering the three mite-infected populations separately, the negative correlation between parasite intensity and winter survival was significant in the Thun (Likelihood ratio test = 13.1, $n = 77$, $p < 0.001$) and in the Nuglar population (Likelihood ratio test = 6.78, $n = 105$, $p = 0.002$). In the Weissenstein population, however, parasite intensity was not related to winter survival (Likelihood ratio test = 0.71, $n = 105$, $p = 0.401$). Winter survival was lower in both the Thun and the Weissenstein populations than in the Nuglar and Allschwil populations (Table 1; $\chi^2 = 23.64$, $df = 1$, $p < 0.001$). In none of the populations was winter survival affected by the size of the snails (Likelihood ratio test, in all cases $p > 0.261$).

Winter survival of infected snails

The percentage of snails that survived the winter was lower in experimentally infected snails (21.9%) than in uninfected snails (44.1%; $\chi^2 = 4.21$, $df = 1$, $p = 0.040$). Winter survival curves differed significantly between experimentally infected and parasite-free snails (Fig. 2; Likelihood ratio test = 8.24, $n = 75$, $p = 0.004$).

Discussion

This study shows that heavily infected individuals of *Arianta arbustorum* are less active and produce fewer eggs than uninfected snails. Furthermore, we show a negative correlation between mite infection and winter survival. The reduced winter survival in experimentally infected snails supports the latter finding.

Life-history theory predicts selection for increased reproductive effort in populations with high extrinsic mortality (Stearns 1992). Parasites that decrease sur-

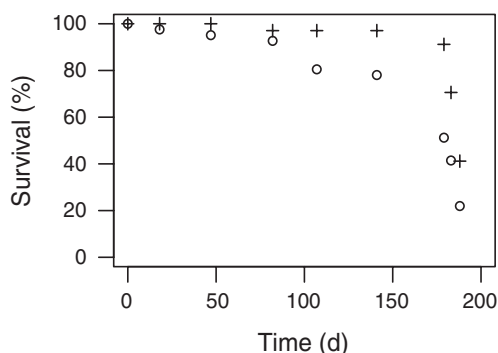


Fig. 2. Survivorship curve of experimentally infected (O) and uninfected (+) individuals of *Arianta arbustorum*, hibernating at 4°C.

vival of iteroparous hosts have an equivalent role, in an evolutionary context, to mortality. Thus, hosts with a high parasite load may show an increased reproductive effort (Minchella & Loverde 1981). Alternatively, parasite pressure might reduce the energy available for the current reproduction, and as a result, infected hosts might exhibit lower life-time fecundity (Møller 1990; Sorci et al. 1996). Our study revealed a reduced reproductive output but a slightly increased hatching success of the eggs deposited by individuals of *A. arbustorum* infected with those of *Riccardoella limacum*. Parasitized snails might shift their allocation of reproductive energy toward egg quality at the expense of egg quantity. The significance of within- and between-clutch variation in egg quality and size, as well as their seasonal changes, have been examined in *A. arbustorum* (Baur 1994; Baur & Baur 1997). However, experimental approaches are needed to demonstrate the effect of parasitic mites on changes in egg quality in *A. arbustorum*.

The main focus of parasite impact concerns life-history traits such as age-specific growth, reproduction, and survival (Stearns 1992). However, parasites can manipulate their host's behavior as well (De Jong-Brink & Koene 2005). As in our study, a strong mite infection in *Cornu aspersum* was associated with extended periods of resting (Graham et al. 1996). The reduced activity of mite-infected members of *A. arbustorum* might be associated with a decreased feeding activity as shown in *C. aspersum*, and might lead to a reduced food uptake. Furthermore, a decreased activity might be associated with a decline in mating frequency, which could restrict outcrossing opportunities. However, the reduced activity could also be a host's response to the parasite pressure, and might help to compensate for the energy and nutrients consumed by the parasite.

The winter survival of *A. arbustorum* was reduced in experimentally infected snails, and we found a negative correlation between parasite intensity and winter survival in two out of three populations. It is not known whether infected snails from the parasite-free population had an increased susceptibility. The mean intensity of mite infection was higher in experimentally infected individuals (4.9 mites; H.U. Schüpbach, unpubl. data) than in naturally infected snails (0.5–1.9 mites; range 0.3–8 mites: Baur & Baur 2005), but it was still in the range of naturally infected individuals. During hibernation, the mortality of infected snails was moderate, but increased strongly after the snails awoke from hibernation. Snails may hibernate with reduced energy reserves. In spring, they might be too weak to reactivate their metabo-

lism, which results in an increased mortality. Correlations between parasite infection and fitness components of the host provide only limited information on the causation of the correlation (Zera 2001). Parasite infection might be the result of the reduced fitness instead of the cause. The experimental data on winter survival, however, show the causality between mite infection and fitness in *A. arbustorum*, and strongly confirm our results from the correlational approach.

There is abundant literature demonstrating the effects of ectoparasites on the survival, reproduction, and population dynamics in vertebrates (Sorci & Clobert 1995; Richner 1998) and insects (Polak 1998; Braune & Rolff 2001). Furthermore, several studies revealed a reduced reproductive performance of marine gastropods infected with parasitic trematodes (Huxham et al. 1993; Fredensborg et al. 2005). Evidently, the parasite pressure imposed by *R. limacum* may differ considerably from that created by castrating endoparasites. However, the impacts of parasitic mites on the individual fitness of terrestrial gastropods and the dynamics of their populations are, as yet, poorly understood. Important aspects of the interaction between members of *R. limacum* and *A. arbustorum*, such as host susceptibility and resistance, transmission biology, and host defense, are still unknown. It is therefore difficult to predict the characteristics of co-evolutionary processes between *R. limacum* and *A. arbustorum*.

A parasite-induced reduction in host fertility and survival has immediate effects on the population dynamics of the host (Jaenike et al. 1995). However, co-evolution might also affect the evolution of the host's life-history traits (Agnew et al. 2000). The negative correlations between parasite infection and winter survival, reproductive output, and behavior of the host, together with the experimental evidence of parasite-induced reduction of winter survival, suggest that parasite pressure may influence life history in *A. arbustorum*.

Acknowledgments. We thank A. Baur, C. Seiberth, and M. Coslovsky for field and laboratory assistance. A. Baur, K. Beese, J. Koene, P. Stoll, and an anonymous reviewer provided valuable comments on the manuscript. Financial support was received from the Swiss National Science Foundation (grant 31-110061).

References

- Agnew P, Koella JC, & Michalakis Y 2000. Host life history responses to parasitism. *Microbes Infect.* 2: 891–896.

- Baker RA 1970a. Studies on the life history of *Riccardoella limacum* (Schränk) (Acari, Trombidiformes). *J. Nat. Hist.* 4: 511–519.
- 1970b. The food of *Riccardoella limacum* (Schränk) (Acari, Trombidiformes) and its relationship with pulmonate molluscs. *J. Nat. Hist.* 4: 521–530.
- Baur A 1994. Within-clutch and between-clutch variation in egg size and nutrient content in the land snail *Arianta arbustorum*. *Funct. Ecol.* 8: 581–586.
- Baur A & Baur B 1997. Seasonal variation in size and nutrient content of eggs of the land snail *Arianta arbustorum*. *Invertebr. Reprod. Dev.* 32: 55–62.
- 2005. Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebr. Biol.* 124: 194–201.
- Baur B 1986. Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). *Holarct. Ecol.* 9: 117–125.
- 1988. Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. *Oecologia* 77: 390–394.
- 1990. Seasonal changes in clutch size, egg size and mode of oviposition in *Arianta arbustorum* L. (Gastropoda) from alpine populations. *Zool. Anz.* 225: 253–264.
- 1994. Multiple paternity and individual variation in sperm precedence in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Behav. Ecol. Sociobiol.* 35: 413–421.
- Baur B & Raboud C 1988. Life-history of the land snail *Arianta arbustorum* along an altitudinal gradient. *J. Anim. Ecol.* 57: 71–87.
- Braune P & Rolff J 2001. Parasitism and survival in a damselfly: does host sex matter? *Proc. R. Soc. London Ser. B.* 268: 1133–1137.
- Chen XF 1994. Self-fertilization and cross-fertilization in the land snail *Arianta arbustorum* (Mollusca, Pulmonata, Helicidae). *J. Zool.* 232: 465–471.
- Day T 2001. Parasite transmission modes and the evolution of virulence. *Evolution* 55: 2389–2400.
- De Jong-Brink M & Koene JM 2005. Parasitic manipulation: going beyond behaviour. *Behav. Processes* 68: 229–233.
- Fain A & van Goethem JL 1986. Les acariens du genre *Riccardoella* Berlese, 1923 parasites du poumon de mollusques gastéropodes pulmonés terrestres. *Acarologia* 27: 125–140.
- Forbes MRL 1993. Parasitism and host reproductive effort. *Oikos* 67: 444–450.
- Fredensborg BL, Mouritsen KN, & Poulin R 2005. Impact of trematodes on host survival and population density in the intertidal gastropod *Zeacumantus subcarinatus*. *Mar. Ecol. Prog. Ser.* 290: 109–117.
- Gandon S, Agnew P, & Michalakis Y 2002. Coevolution between parasite virulence and host life-history traits. *Am. Nat.* 160: 374–388.
- Goater CP, Semlitsch RD, & Bernasconi MV 1993. Effects of body size and parasite infection on the locomotory

- performance of juvenile toads, *Bufo bufo*. *Oikos* 66: 129–136.
- Graham F 1994. The biology and control of *Riccardoella limacum* (Schränk), a mite pest of farmed snails. PhD thesis, University of Wales.
- Graham FJ, Runham NW, & Ford JB 1996. Long-term effects of *Riccardoella limacum* living in the lung of *Helix aspersa*. *BCPC Symp. Proc.* 66: 359–364.
- Hochberg ME, Michalakis Y, & de Meeus T 1992. Parasitism as a constraint on the rate of life-history evolution. *J. Evol. Biol.* 5: 491–504.
- Huxham M, Raffaelli D, & Pike A 1993. The influence of *Cryptocotyle lingua* (Digenea: Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia)—an ecological approach. *J. Exp. Mar. Biol. Ecol.* 168: 223–238.
- Jaenike J, Benway H, & Stevens G 1995. Parasite-induced mortality in mycophagous *Drosophila*. *Ecology* 76: 383–391.
- Jokela J, Taskinen J, Mutikainen P, & Kopp K 2005. Virulence of parasites in hosts under environmental stress: experiments with anoxia and starvation. *Oikos* 108: 156–164.
- Kerney M & Cameron R 1979. *A Field Guide to the Land Snails of Britain and North-West Europe*. Collins, London, UK.
- Koella JC & Restif O 2001. Coevolution of parasite virulence and host life history. *Ecol. Lett.* 4: 207–214.
- Krist AC 2006. Prevalence of parasites does not predict age at first reproduction or reproductive output in the freshwater snail, *Helisoma anceps*. *Evol. Ecol. Res.* 8: 753–763.
- Minchella DJ & Loverde PT 1981. A cost of increased early reproductive effort in the snail *Biomphalaria glabrata*. *Am. Nat.* 118: 876–881.
- Minchella DJ & Scott ME 1991. Parasitism—a cryptic determinant of animal community structure. *Trends Ecol. Evol.* 6: 250–254.
- Mitchell SE, Rogers ES, Little TJ, & Read AF 2005. Host-parasite and genotype-by-environment interactions: temperature modifies potential for selection by a sterilizing pathogen. *Evolution* 59: 70–80.
- Møller AP 1990. Effects of parasitism by a haematophagous mite on reproduction in the Barn Swallow. *Ecology* 71: 2345–2357.
- Oosterhoff LM 1977. Variation in growth rate as an ecological factor in the land snail *Cepaea nemoralis* (L.). *Neth. J. Zool.* 27: 1–132.
- Perrin N, Christe P, & Richner H 1996. On host life-history response to parasitism. *Oikos* 75: 317–320.
- Polak M 1998. Effects of ectoparasitism on host condition in the *Drosophila-Macrocheles* system. *Ecology* 79: 1807–1817.
- R Development Core Team 2006. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Restif O, Hochberg ME, & Koella JC 2001. Virulence and age at reproduction: new insights into host–parasite coevolution. *J. Evol. Biol.* 14: 967–979.
- Richner H 1998. Host–parasite interactions and life-history evolution. *Zoology* 101: 333–344.
- Sorci G & Clobert J 1995. Effects of maternal parasite load on offspring life-history traits in the common lizard (*Lacerta vivipara*). *J. Evol. Biol.* 8: 711–723.
- Sorci G, Clobert J, & Michalakis Y 1996. Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos* 76: 121–130.
- Stearns SC 1992. *The Evolution of Life History*. Oxford University Press, Oxford.
- Turk FA & Phillips SM 1946. *A monograph of the slug mite—Riccardoella limacum* (Schränk). *Proc. Zool. Soc. London* 115: 448–472.
- Zera AJ 2001. The physiology of life history trade-offs in animals. *Annu. Rev. Ecol. Evol. Syst.* 32: 95–126.

CHAPTER 2

Within- and among-family variation in parasite load and
parasite-induced mortality in the land snail *Arianta*
arbustorum, a host of parasitic mites

Hans Ulrich Schüpbach and Bruno Baur

Journal of Parasitology (2010), in press

RESEARCH NOTE

Within- and among-family variation in parasite load and parasite-induced mortality in the land snail *Arianta arbustorum*, a host of parasitic mites

Hans Ulrich Schüpbach and Bruno Baur, Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johannis-Vorstadt 10, CH-4056 Basel, Switzerland. *e-mail: H.Schuepbach@unibas.ch*

ABSTRACT: Variation in host susceptibility and parasite-induced mortality are preconditions for parasite-related selection on host populations. In terrestrial gastropods, variation in resistance against ectoparasite infection is poorly understood. We examined the within- and among-family variation in parasite load in full-siblings of the land snail *Arianta arbustorum* experimentally infected with *Riccardoella limacum*, a mite living in the mantle cavity of helioid land snails. We also quantified the influence of family origin and host size on parasite load and calculated its heritability (h^2). Furthermore, we examined the influence of parasite load, snail size, and family origin on host winter mortality, an important life-history trait of *A. arbustorum*. Parasite load was heritable ($h^2 = 0.63$). In infected snails, parasite load was affected by family origin and increased with increasing shell size. Host mortality during hibernation increased with increasing parasite load and differed among families, but was not affected by snail size. Our results show high among-family variation both in resistance against ectoparasite infection and in host winter mortality. Furthermore, we show that parasite load is linked to snail size, which suggests that the proliferation of *R. limacum* is limited by resources provided by *A. arbustorum*.

Additive genetic variation in host resistance against parasite infection is a key assumption in models of host-parasite coevolution and is a prerequisite for parasite-induced selection on host populations (Mitchell et al., 2005; Little et al., 2006). Variation in host susceptibility (Grenfell et al., 2004) and parasite-induced effects on host survival

and fertility (Jaenike et al., 1995) may influence the epidemiology of host-parasite systems (Agnew et al., 2000). Mechanisms enabling vertebrate hosts to resist against ectoparasite infection have received considerable attention (e.g., Christe et al. 2000; Wikel and Alarcon-Chaidez, 2001; Roulin et al., 2007). The plasticity of their adaptive immune system promotes a high variability in the genetic background allowing hosts to cope with parasite infection (Lazzaro and Little, 2009). In invertebrate hosts, the genetic background of resistance against ectoparasites is much less studied (Wikel and Alarcon-Chaidez, 2001). Knowledge on heritability in parasite resistance mainly originates from insect hosts (Polak, 2003; Luong et al., 2007). However, in other taxa such as terrestrial gastropods, the heritability of resistance against ectoparasites is poorly understood.

The mite *Riccardoella limacum* is a monoxenous ectoparasite of land snails (Fain and van Goethem, 1986). The parasite feeds on blood in the mantle cavity of its host. Individuals of *R. limacum* regularly leave the mantle cavity and can be observed moving over the soft body of their host. Transmission occurs during host contact and via mucus trails of the host snail (Schüpbach and Baur, 2008a). In the land snail, *Arianta arbustorum*, *R. limacum* reduced both the reproductive output and winter survival of its host (Schüpbach and Baur, 2008b). The aims of our study were (1) to quantify the variation in parasite susceptibility measured by the parasite load in experimentally infected individuals of *A. arbustorum* derived from different families, and (2) to assess the parasite-induced mortality within and among snail families and the potential effect of individual snail size.

Family arrays were obtained from single mated mother snails collected in a parasite-free population in Gurnigelbad near Bern, Switzerland (46°45' N, 7°27' E; elevation 1,330 m). From each of 15 snails, 2 egg batches (mean number of eggs per batch 31.7 ± 2.2 eggs) were collected and incubated at 19 ± 1 C. The hatchlings were kept in groups of 8 snails in transparent plastic beakers (6.4 cm in diameter, 2.2 cm deep) on moist soil mixed with powdered limestone under a light:dark regime of 16 : 8 hr and a constant temperature of 19 ± 1 C. The beakers were cleaned 1–2 times per wk and a diet of fresh lettuce was provided ad libitum. After 12 wk, we randomly chose 12 snails from each snail family. Four siblings were hereafter kept together in larger containers (8 cm in

diameter, 9 cm deep) lined with soil. Before attaining sexual maturity, snails were placed individually in transparent plastic beakers (6.5 cm in diameter, 8 cm deep) lined with soil (see above). After reaching maturity indicated by the formation of a reflected shell lip, the individuals of each family were visually sorted according to decreasing shell size and consecutively numbered (1–12). Every second snail of each family was then infected with *R. limacum*, the remaining 6 snails served as uninfected control.

Mites were obtained from parasite-infected individuals of *A. arbustorum* collected in Nuglar, near Basel (47°29' N, 7°42' E; elevation 430 m). With a small, moistened paintbrush, 6 adult mites were transferred to the soft body of an uninfected snail. We waited until the mites entered the mantle cavity of the new host. Transmitted mites were allowed to reproduce on their host for 6 wk (2 mite generations; Graham et al., 1996). Then, we assessed the infection status and parasite load of both infected and control snails using a non-invasive screening method (Baur and Baur, 2005). The soft body and respiratory pore of each individual were carefully examined for mites using a magnifying glass (10x). Mite screening was repeated 3 times on different days. A snail was considered as parasite-infected if at least 1 mite could be detected in 3 observations. The parasite load was expressed as the mean number of mites observed in the 3 examinations (Baur and Baur, 2005).

We used the snail identification number (1–12) as a measure of relative snail size in each family (1 = largest snail, 12 = smallest snail within family). In a subsample of 24 snails distributed over all families and identification numbers, we measured the shell breadth and height of the individuals to the nearest 0.1 mm using a vernier caliper and calculated shell volume using the formula: shell volume = $0,312 \times [(\text{shell breadth})^2 \times \text{shell height}] - 0.0388$ (B. Baur, unpubl. obs.). Shell volume is a more reliable measurement of snail size than mass, because mass depends on the state of hydration and thus is highly variable in terrestrial gastropods.

Infected and control snails were allowed to hibernate at 4 C and darkness in beakers lined with 4 cm moist soil (no food was provided). These conditions are similar to those of hibernating snails buried in soil in the field (Baur, 1994). Hibernating snails were checked every second week to record dead animals. Hibernation lasted 24 wk, as occurs

in natural sub-alpine populations (Baur, 1986). After this period, the snails were aroused by resetting the temperature, light regime, and food supply to the conditions before hibernation. We recorded dead animals for another 3 wk after the snails emerged from hibernation.

We used mixed effect models to analyze the influence of family origin (random factor) and relative snail size on the parasite load. The relative size was implemented as a factor consisting of 3 size classes nested within snail family (large, snail no. 1–4; medium, snail no. 5–8; small, snail no. 9–12). Furthermore, we estimated the heritability (h^2) of the parasite load by calculating the within- and among-family components of variance from one-way ANOVAs (Falconer and Mackay, 1996). The dominance variance within full-sib snails was not considered and consequently our estimate represents the upper limit of the actual heritability (Falconer and Mackay, 1996). We used Cox's proportional hazard regression models for the survival analyses. Means \pm SE are reported.

In total, we infected 85 snails from 15 families with *R. limacum*. Three snails (3.5%) were excluded from the analysis because we could not detect any mites. Furthermore, we excluded 21 snails that died before parasite screening. Six wk after experimental infection, the mean parasite load in infected snails was 4.99 ± 0.45 mites ($n = 61$). None of the control snails had any mites. Parasite load was significantly affected by family origin ($F_{14,46} = 2.68$, $P = 0.020$; Fig. 1) and by snail size nested within family ($F_{2,58} = 2.44$; $P = 0.021$; Fig. 2). Parasite load was highest in snails of the large size class (6.86 ± 0.90 mites), moderate in snails of the medium size class (4.35 ± 0.57 mites) and relatively low in snails of small size (3.5 ± 0.71 mites). Furthermore, in the subsample parasite load was positively correlated with shell volume (Pearson's correlation: $r = 0.51$, $n = 24$, $P = 0.010$).

The heritability (h^2) of parasite load (the proportion of phenotypic variation that is attributable to genetic variation) was 0.62 ± 0.16 ($F_{14,46} = 2.68$, $P = 0.020$).

A total of 128 snails from 15 families was allowed to hibernate; 61 (47.7%) of them were infected with *R. limacum*. Winter mortality was significantly affected by parasite load (Likelihood-ratio chi-square test: $\chi^2 = 3.89$, $df = 1$, $P = 0.049$; Fig. 3) and family origin ($\chi^2 = 43.15$, $df = 14$, $P = 0.002$). Snail mortality was 94.4% in infected and 73.8%

in uninfected snails. However, mortality was not affected by snail size ($\chi^2 = 1.57$, $df = 2$, $P = 0.46$).

Parasite load of experimentally infected *A. arbustorum* revealed a high variation among snail families. Phenotypic resemblance among full siblings under experimental conditions implies that inherited genetic variation may cause this difference (Falconer and Mackay, 1996). The high heritability indicates a strong impact of the genetic background on the parasite load. However, further aspects including maternal effects may contribute to the parasite resistance in the offspring (Little et al., 2006). Furthermore, we did not consider possible effects of phenotypic variance caused by the dominance variance among full sibs (Falconer and Mackay, 1996).

Within snail family parasite load increased with increasing shell size. This suggests that size-linked resources provided by *A. arbustorum* may limit the growth of *R. limacum* cohorts. Availability of food resources is essential for the proliferation of parasite cohorts in invertebrate hosts (Pulkkinen and Ebert, 2004). However, cohort growth of *R. limacum* might also be impeded by spatial limitations in the mantle cavity either for egg deposition or feeding sites of larval and adult mites.

Host mortality during hibernation was affected by both parasite load and family origin. Because snail size did not affect mortality of *A. arbustorum*, it is unlikely that the size effect on parasite load is an artifact caused by an intercorrelation between size and snail fitness. Snail mortality was higher in both infected and control snails compared to snails from natural populations hibernating under identical conditions (Schüpbach and Baur, 2008b). The favorable conditions of snail rearing in the laboratory may strongly contrast selection pressures occurring under natural conditions. In our experiment, mortality might, therefore, be shifted from adolescence towards the hibernation period.

Differences in mortality of parasitized and parasite-free hosts may directly affect gene frequencies in the host population and thus influence the host-parasite coevolution (Mitchell et al., 2005). Furthermore, the high variation in parasite load and winter mortality among snails might influence the genetic composition and thus seriously affect the population structure of *A. arbustorum*.

We thank N. Lang and M. Coslovsky for laboratory assistance and A. Baur for comments on the manuscript. Financial support was received from the Swiss National Science Foundation (grant 31-110061).

LITERATURE CITED

- AGNEW, P., J. C. KOELLA, AND Y. MICHALAKIS. 2000. Host life history responses to parasitism. *Microbes and Infection* **2**: 891–896.
- BAUR, A., AND B. BAUR. 2005. Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebrate Biology* **124**: 194–201.
- BAUR, B. 1986. Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L) (Helicidae). *Holarctic Ecology* **9**: 117–125.
- _____. 1994. Multiple paternity and individual variation in sperm precedence in the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Behavioral Ecology and Sociobiology* **35**: 413–421.
- CHRISTE, P., R. ARLETTAZ, AND P. VOGEL. 2000. Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). *Ecology Letters* **3**: 207–212.
- FAIN, A., AND J. L. VAN GOETHEM. 1986. Les acariens du genre *Riccardoella* Berlese, 1923 parasites du poumon de mollusques gastéropodes pulmonés terrestres. *Acarologia* **27**: 125–140.
- FALCONER, D. S., AND T. F. C. MACKAY. 1996. Introduction to quantitative genetics. 4th ed. Longman Group Limited, Essex, England.
- GRAHAM, F. J., N. W. RUNHAM, J. B. FORD, AND I. F. HENDERSON. 1996. Long-term effects of *Riccardoella limacum* living in the lung of *Helix aspersa*. BCPC Symposium Proceedings **66**: 359–364.
- GRENFELL, B. T., J. R. PYBUS, J. R. GOG, J. L. N. WOOD, J. A. MUMFORD. AND E. C. HOLMES. 2004. Unifying the epidemiological and evolutionary dynamics of pathogens. *Science* **303**: 327–332.

- JAENIKE, J., H. BENWAY, AND STEVENS, G. 1995. Parasite-induced mortality in mycophagous *Drosophila*. *Ecology* **76**: 383–391.
- LAZZARO, B. P., AND T. J. LITTLE. 2009. Immunity in a variable world. *Philosophical Transactions of the Royal Society B-Biological Sciences* **364**: 15–26.
- LITTLE, T. J., K. WATT, AND D. EBERT. 2006. Parasite-host specificity: Experimental studies on the basis of parasite adaptation. *Evolution* **60**: 31–38.
- LUONG, L. T., B. D. HEATH, AND M. POLAK. 2007. Host inbreeding increases susceptibility to ectoparasitism. *Journal of Evolutionary Biology* **20**: 79–86.
- MITCHELL, S. E., E. S. ROGERS, T. J. LITTLE, AND A. F. READ. 2005. Host-parasite and genotype-by-environment interactions: Temperature modifies potential for selection by a sterilizing pathogen. *Evolution* **59**: 70–80.
- POLAK, M. 2003. Heritability of resistance against ectoparasitism in the *Drosophila*-*Macrocheles* system. *Journal of Evolutionary Biology* **16**: 74–82.
- PULKKINEN, K., AND D. EBERT. 2004. Host starvation decreases parasite load and mean host size in experimental populations. *Ecology* **85**: 823–833.
- ROULIN, A., P. CHRISTE, C. DIJKSTRA, A. L. DUCREST, AND T. W. JUNGI. 2007. Origin-related, environmental, sex, and age determinants of immunocompetence, susceptibility to ectoparasites, and disease symptoms in the barn owl. *Biological Journal of the Linnean Society* **90**: 703–718.
- SCHÜPBACH, H.U., AND B. BAUR. 2008a. Experimental evidence for a new transmission route in a parasitic mite and its mucus-dependent orientation towards the host snail. *Parasitology* **135**: 1679–1684.
- _____, AND _____. 2008b. Parasitic mites influence fitness components of their host, the land snail *Arianta arbustorum*. *Invertebrate Biology* **127**: 350–356.
- WIKEL, S. K., AND F. J. ALARCON-CHAIDEZ. 2001. Progress toward molecular characterization of ectoparasite modulation of host immunity. *Veterinary Parasitology* **101**: 275–287.

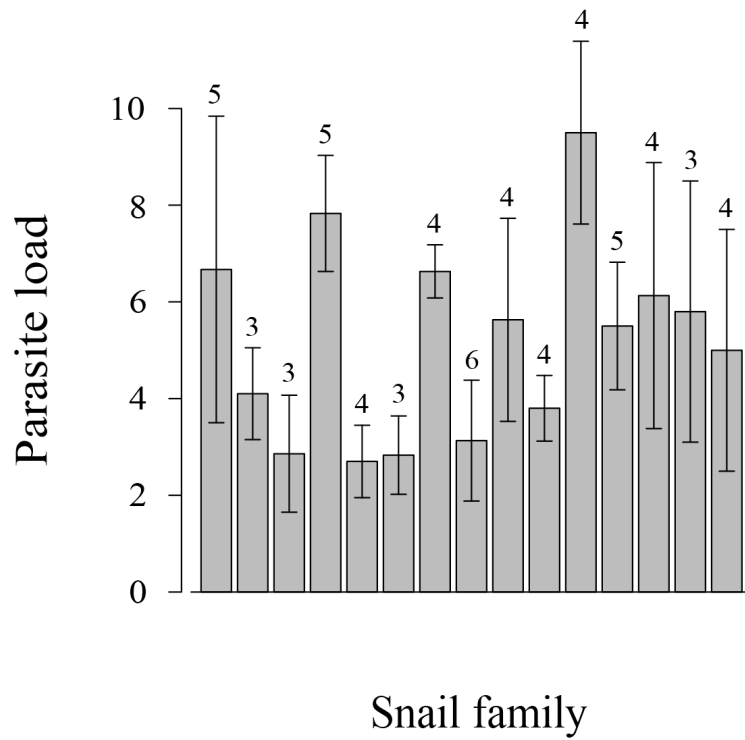


FIGURE 1. Parasite load (means \pm S.E.) of 15 snail families of *Arianta arbustorum* experimentally infected with *Riccardoella limacum*. Figures on top of bars indicate the number of siblings per family. The parasite load differed significantly among snail families.

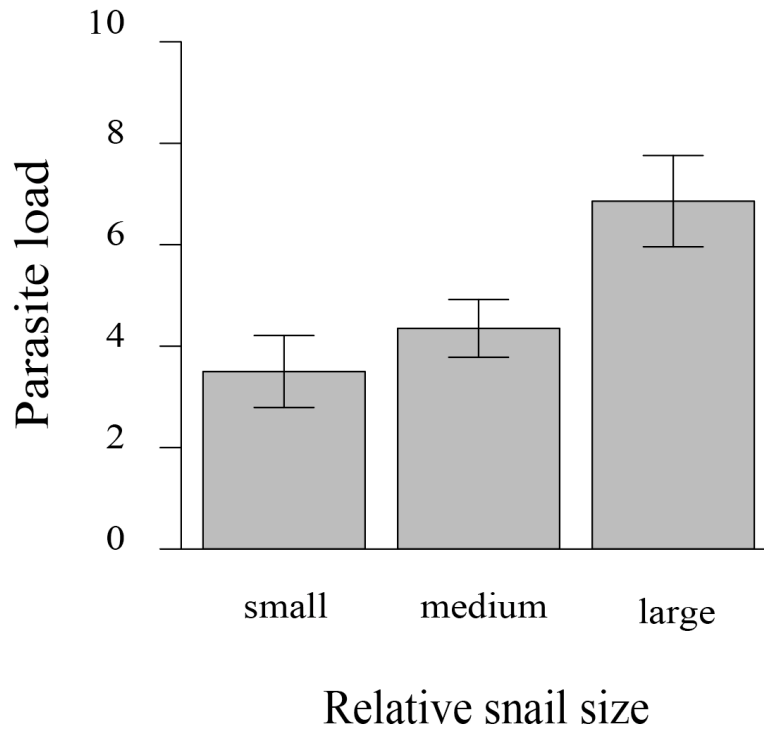


FIGURE 2. Parasite load (means \pm S.E.) of 3 size classes (small, medium, large) of *Arianta arbustorum* experimentally infected with *Riccardoella limacum*. The relative size allows a comparison of siblings from different snail families. Parasite load increased with increasing relative snail size.

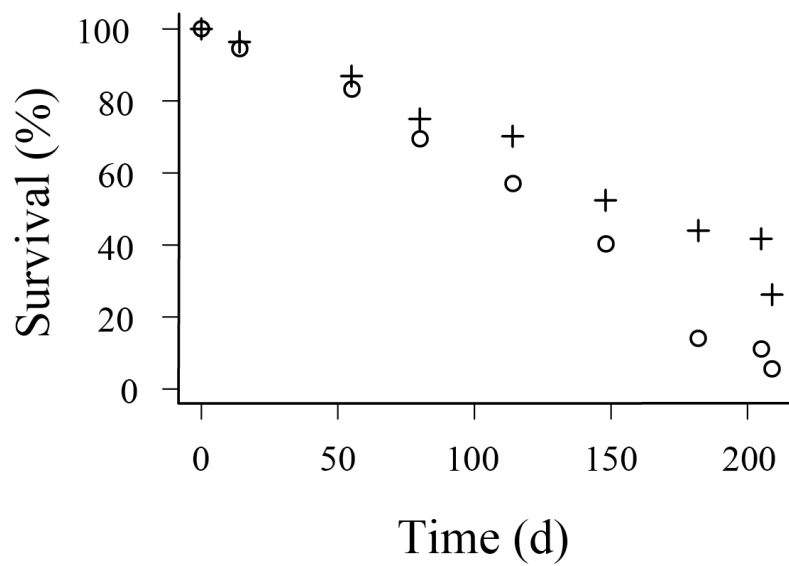


FIGURE 3. Survival curves of infected (o) and uninfected (+) *Arianta arbustorum* hibernating at 4 C. Mortality was higher in infected than in uninfected snails.

CHAPTER 3

Experimental evidence for a new transmission route in a
parasitic mite and its mucus-dependent orientation towards the
host snail

Hans Ulrich Schüpbach and Bruno Baur

Parasitology (2008) 135: 1679–1684

Experimental evidence for a new transmission route in a parasitic mite and its mucus-dependent orientation towards the host snail

H. U. SCHÜPBACH* and B. BAUR

Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St Johannis-Vorstadt 10, CH-4056 Basel, Switzerland

(Received 26 June 2008; revised 5 August 2008; accepted 25 August 2008)

SUMMARY

The route of transmission and host finding behaviour are fundamental components of a parasite's fitness. *Riccardoella limacum*, a haematophagous mite, lives in the mantle cavity of helioid land snails. To date it has been assumed that this parasitic mite is transmitted during courtship and mating of the host. Here we present experimental evidence for a new transmission route in the host snail *Arianta arbustorum*. Parasite-free snails were kept on soil on which previously infected host snails had been maintained for 6 weeks. *R. limacum* was successfully transmitted via soil without physical contact among hosts in 10 out of 22 (45.5%) cases. In a series of experiments we also examined the off-host locomotion of *R. limacum* on snail mucus and control substrates using an automated camera system. Parasitic mites showed a preference to move on fresh mucus. Our results support the hypothesis that *R. limacum* uses mucus trails to locate new hosts. These findings should be considered in commercial snail farming and when examining the epidemiology of wild populations.

Key words: parasite transmission, host-finding, snail mucus, *Arianta arbustorum*, *Riccardoella limacum*.

INTRODUCTION

Parasite transmission in a host population is a fundamental component of the parasite's fitness (Fenton *et al.* 2002; Galvani, 2003), and is closely linked to other traits such as fecundity, survival and virulence (Bull, 1994; Ebert and Herre, 1996; Crossan *et al.* 2007). In macroparasites, the transmission between hosts is often actively occurring during host contact or through mobile, free-living stages of the parasite (Combes, 2001). Since suitable hosts are patchily distributed in space and time, the optimal strategy for transmission depends on both the mechanisms of parasite transmission (Fenton and Rands, 2004; Robb and Forbes, 2005) and on the spatial structure of the host population (Boots and Meador, 2007; Crossan *et al.* 2007). Differences in mechanisms of transmission and pathogenesis may lead to pronounced differences in the epidemiology of the interacting species (Ganusov and Antia, 2003; Frank and Schmid-Hempel, 2008). Strong selection pressure on parasites to develop optimal strategies in order to maximize their likelihood of successful transmission may therefore be expected (Fenton and Rands, 2004; Poulin, 2007). A possible strategy to increase the probability of transmission and to locate new hosts is the use of signals from the environment

or from the host (Rea and Irwin, 1994; Krasnov *et al.* 2002; Hertel *et al.* 2006).

The mite *Riccardoella limacum* (SCHRANK 1776) is a monoxenous ectoparasite of land snails (Fain and Van Goethem, 1986). The parasite feeds on blood in the mantle cavity of its host. Heavy infestation with *R. limacum* reduces the growth rate and delays reproductive development in the snail *Cornu aspersum* (MÜLLER 1774). These adverse effects can seriously influence the economy of commercial snail farming (Graham, 1994; Graham *et al.* 1996). In the land snail *Arianta arbustorum* (LINNAEUS 1758), *R. limacum* reduced both the reproductive output and winter survival of its host (Schüpbach and Baur, 2008). However, little is known about the transmission biology of the parasitic mite. The mite is actively transmitted during courtship and mating of the host *A. arbustorum*. Mites leave the mantle cavity, move over the soft body of the snail, and switch to the new host. However, mites have also been observed in juvenile snails (Baur and Baur, 2005), suggesting other ways of parasite transmission. Individuals of *R. limacum* might also disperse via soil. Daily movements and dispersal of *A. arbustorum* are restricted to a rather narrow range (Baur, 1986; Baur and Baur, 1993). This may enhance the parasite's probability to locate new hosts. Furthermore, snails secrete mucus during locomotion. The adhesive and lubricant characteristics of mucus permit adhesion to the substrate and snail locomotion (Barker, 2001).

* Corresponding author: Tel: +41 61 267 08 44. Fax: +41 61 267 08 32. E-mail: H.Schuepbach@unibas.ch

Mucus is also important for the communication among snails. Mucus trails could be used by *R. limacum* to find new hosts.

The aim of our study was to investigate the transmission biology of *R. limacum*. We experimentally tested whether *R. limacum* is successfully transmitted via soil without physical contact among host individuals. We also examined the off-host locomotion of *R. limacum*. In particular, we tested whether locomotion of *R. limacum* is affected by mucus trails of the host.

MATERIALS AND METHODS

Study species

Riccardoella limacum is a parasitic mite that lives in the mantle cavity of helioid land snails (Fain and Van Goethem, 1986; Graham *et al.* 1993). The parasite's life cycle has been studied under laboratory conditions in the host snail *Cornu aspersum* (Graham, 1994). Female mites lay their eggs in the respiratory tissue of their host. Three nymphal mite stages are followed by sexually mature males and females, both 0.4 mm in body length (Baker, 1970a). The total life cycle of *R. limacum* lasts 19–23 days at temperatures of 20–25 °C. During hibernation of the host, adult mites rarely survive in the mantle cavity, but a new generation of larvae emerges from overwintered eggs in spring. *R. limacum* is a blood-sucking parasite (Baker, 1970b), which causes considerable harm in *C. aspersum* by reducing the activity and the growth rate and delaying reproductive development (Graham *et al.* 1996).

Arianta arbustorum, a common host of *R. limacum*, is a simultaneously hermaphroditic helioid land snail common in moist habitats of northwestern and central Europe (Kerney and Cameron, 1979). The snail has determinate growth (shell breadth of adults 16–24 mm). Individuals become sexually mature at an age of 2–4 years and live for another 3–4 years (Baur and Raboud, 1988). Individuals usually reproduce through outcrossing. Mating includes elaborate courtship and lasts 2–18 h (Baur, 1992).

A considerable variation in prevalence and intensity of *R. limacum* infection was found in wild *A. arbustorum* populations in Switzerland (Baur and Baur, 2005). The parasite occurred in 4 out of 11 populations examined, with a prevalence of 45.8–77.8%. The infection with *R. limacum* affects the life-history and behaviour of *A. arbustorum* (Schüpbach and Baur, 2008). Infected hosts laid fewer eggs and were less active. Furthermore, in 2 out of 3 populations and in experimentally infected snails, hosts suffered an increased mortality during hibernation compared to uninfected snails.

During the long-lasting mating of host snails, *R. limacum* moves from parasite-infected snails to the mating partner (H. U. Schüpbach, personal

observation). However, mite infection sporadically occurs in juvenile snails (Baur and Baur, 2005), suggesting other types of parasite transmission.

Experiment 1: Parasite transmission

We collected 22 mite-infected snails (hereafter referred to as infected snails) in Nuglar (47°29'N, 7°42'E; elevation 430 m), and 24 snails in a parasite-free population near Gurnigelbad (46°45'N, 7°27'E; elevation 1330 m), in Switzerland. The snails were kept individually in transparent plastic beakers (6.5 cm in diameter, 8 cm deep) on moist soil mixed with powdered limestone under a light:dark regime of 16:8 h and a constant temperature of 19±1 °C. The soil was obtained from the locality Gurnigelbad where *R. limacum* may not occur (Baur and Baur, 2005). The beakers were cleaned 1–2 times per week and a diet of fresh lettuce was provided *ad libitum*. To test whether the transmission of *R. limacum* can occur without physical contact of hosts, the infected snails were removed from the beakers after 6 weeks and replaced by parasite-free snails (hereafter referred to as test snails) from the Gurnigelbad population ($n=46$). Test snails were checked for mites after being kept for 6 weeks in the beakers of the infected snails.

The infection status and intensity of infection of both the infected and test snails were assessed using a non-invasive screening method (Baur and Baur, 2005). The soft body and respiratory pore of each individual were carefully examined for mites using a magnifying glass (10×). Mite screening was repeated 3 times on different days. A snail was considered as parasite-infected if at least 1 mite could be detected in 3 observations. The intensity of infection was expressed as the mean number of mites observed in the 3 examinations (Baur and Baur, 2005).

Experiments 2–4: Mite locomotion

General method. We applied an automated camera system to examine whether the off-host locomotion of *R. limacum* is affected by the presence of snail mucus. We used a template with a round hole in the centre (5.4 mm in diameter) to coat a defined area of a microscope slide with fresh mucus (Fig. 1). After removing the template we placed a mite in the centre of the mucus spot. Mites were transferred with a small, moistened paintbrush from the soft body of infected snails collected in Nuglar (see above). Fresh mucus was obtained from the same snail from which the mite was collected. Immediately after transfer, the movement of the mite was recorded with a digital camera (Canon PowerShot S70) mounted on a stereomicroscope. We took 15 photographs with a frame of 1 sec. The photographs were analysed using the image processing software ImageJ (NIH, USA;

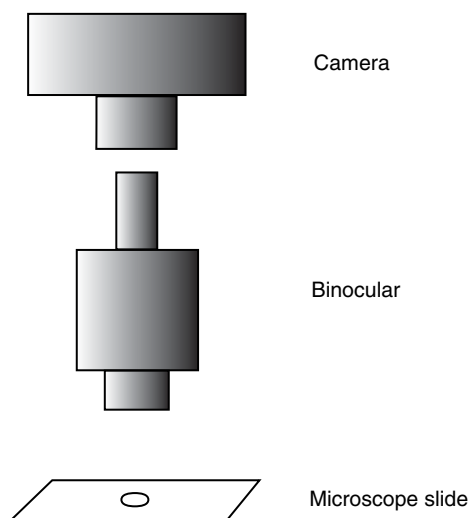


Fig. 1. Assay for studying movement patterns of *Riccardoella limacum*. Mite movement on microscope slide (76 × 26 mm) was photographed at 1-sec intervals. Treatments were applied in the central area (diameter 5.4 mm) of microscope slides.

Version 1.36b; <http://rsb.info.nih.gov/ij/>). We used the template to mark the central area of the microscope slide, and recorded the locomotion of the mite on the photographs. For each mite we calculated the proportion of photographs (out of 15) on which the mite stayed within the defined central area. We also measured the distance moved by the mite between 2 consecutive photographs.

Experiment 2: Mite locomotion on fresh mucus

We used the automated camera system to examine whether mite locomotion is influenced by fresh snail mucus or dry mucus. We covered the central area of the microscope slides with fresh mucus in the first treatment and with dry mucus in the second treatment. Blank microscope slides were used as control. Twenty-two individual mites were tested in each treatment and control, and the percentage of photographs on which the mite stayed in the central area was assessed for each mite (see general method).

Experiment 3: Humidity and mite locomotion

Mite locomotion on fresh mucus could be a result of the humidity of this substrate rather than other characteristics of snail mucus. To distinguish between these two alternatives, we covered the microscope slides with a thin paper towel (Kimberley-Clark, Precision Wipes) moistened with 90 μ l of water before two treatments were prepared. Then 17 mites were tested twice on slides with a mucus spot in the central area (treatment 1) and on moist slides without mucus (control). The sequence in which individual mites were tested was alternated between

the treatments. Data recording was as described above.

Experiment 4: Movement patterns of mites

We also examined whether the locomotion patterns of mites on fresh mucus differs from that on a moist surface. Two aspects of locomotion were considered (i) the distance moved per time unit by a mite and (ii) the directedness of locomotion. We covered the microscope slides with moistened paper towel (see Exp. 3). In contrast to Exp. 3, however, the entire slide was covered with fresh mucus (treatment). As the control we used slides covered with moistened paper towel. A total of 16 mites were tested on both substrates (alternating sequences). Using series of 15 photographs made at 1-sec intervals we measured the distance moved by each mite between 2 consecutive photographs and calculated the mean distance covered per sec for each mite. Furthermore, we measured the angles between the directions of the movement between 2 consecutive photographs. If the movement of a mite is directed, then the distribution of angles between 2 consecutive 1-sec steps will vary around 180°. If mite movement is random, then the distribution of angles between consecutive steps will follow a uniform distribution. To compare mite locomotion on different substrates, the mean angle and the resultant mean vector were calculated for each test series (Batschelet, 1981).

Statistical analysis

Data analysis was performed using R Statistical Software (R Development Core Team, 2008). We used chi-square tests (Exp. 2) and repeated measure ANOVA models (Exp. 3) to compare the proportions of photographs on which the mite stayed in the central area. In Exp. 4, we used Rayleigh tests to evaluate the directedness of angular data (Batschelet, 1981). Means \pm S.E. are reported.

RESULTS

Experiment 1: Parasite transmission

Parasitic mites can be transmitted via soil. Ten out of 22 originally parasite-free snails (45.5%) were infected after being maintained for 6 weeks on soil on which parasite-infected snails were previously kept. The mean intensity of infection was 1.32 ± 0.22 mites in the originally infected snails and 3.20 ± 0.76 mites in the newly infected test snails. The mite-intensity of originally infected snails and those of infected test snails kept later in the same beakers were not correlated (Pearson's correlation: $r = -0.27$, $n = 10$, $P = 0.453$). As expected, no mite transmission occurred from soil of uninfected snails to test snails ($n = 24$).

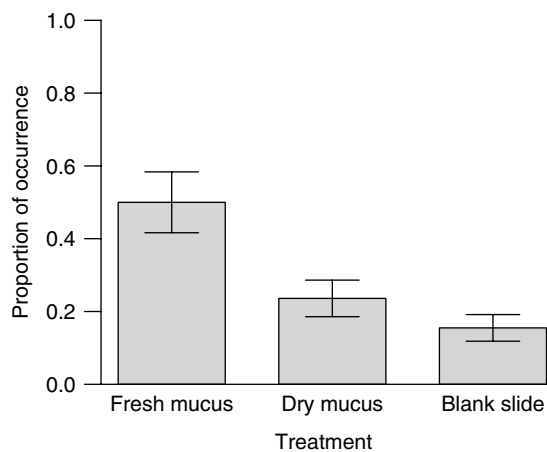


Fig. 2. Proportion of photographs (means ± 1 S.E.) where mites stayed within the defined central area of microscope slides provided with fresh mucus, dry mucus and on blank microscope slides.

Experiment 2: Mite locomotion on fresh mucus

Fresh mucus appears to affect parasite locomotion. The proportion of photographs on which the mite stayed within the defined area was 0.50 ± 0.08 on slides with fresh mucus, 0.23 ± 0.05 on slides with dry mucus and 0.16 ± 0.04 on blank slides (Fig. 2). The difference was significant between fresh mucus and dry mucus ($\chi^2 = 5.12$, D.F. = 1, $P = 0.024$) and between fresh mucus and blank slides ($\chi^2 = 8.33$, D.F. = 1, $P = 0.004$). However, there was no difference in mite locomotion between slides with dry mucus and blank slides ($\chi^2 = 1.17$, D.F. = 1, $P = 0.279$).

Experiment 3: Humidity and mite locomotion

The mean proportion of photographs where the mite stayed within the defined central area was significantly higher on microscope slides provided with fresh mucus (0.48 ± 0.09) than on moist slides without mucus (0.24 ± 0.07 ; $F_{1,15} = 14.41$, $P = 0.002$). This indicates that *R. limacum* shows a preference for fresh mucus as a substrate for locomotion. However, there was a significant interaction between the test sequence and the main effect (Fig. 3; $F_{1,15} = 8.91$, $P = 0.009$).

Experiment 4: Movement patterns of mites

Individual mites ($n = 16$) did not differ in the mean distance moved on slides covered by fresh mucus (0.93 ± 0.11 mm) and on slides covered by moist paper towel (1.05 ± 0.09 mm; $F_{1,14} = 1.62$, $P = 0.224$). Furthermore, the interaction between mean distance moved and treatment sequence was not significant ($F_{1,15} = 1.07$, $P = 0.319$). On snail mucus, random movement patterns (Rayleigh test: $P > 0.05$) were

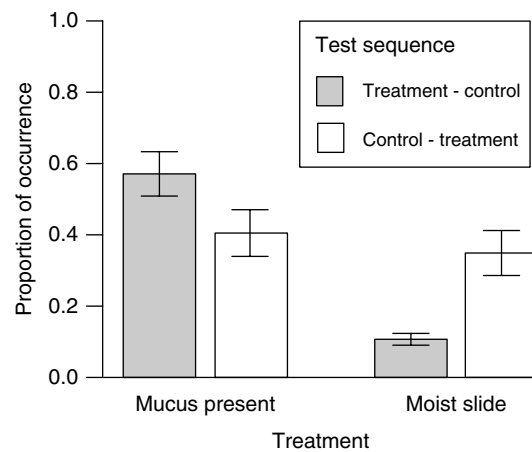


Fig. 3. Proportion of photographs (means ± 1 S.E.) where mites stayed within the defined central area on moistened surfaces provided with fresh mucus or without mucus. Each mite ($n = 17$) was tested in both treatments with alternating test sequences. The mites showed a preference for fresh mucus as a substrate for locomotion, but there was a significant interaction between treatment and the test sequence.

recorded in 3 mites (18.75%), and directed movements (Rayleigh test: $P < 0.05$) in 13 mites (81.25%). Similarly, on moist paper towel, random movement patterns were found in 4 mites (25%), and directed movements in 12 mites (75%). The two substrates did not differ in the proportions of mites moving in a random pattern or in a directed way (chi-square test: $\chi^2 = 0.18$, D.F. = 1, $P = 0.669$).

DISCUSSION

Our study provides experimental evidence that *R. limacum* can be transmitted via soil without physical contact between hosts. Furthermore, *R. limacum* showed a preference to move on fresh snail mucus in the experiment.

R. limacum depends on its host to complete the life cycle. Food uptake and reproduction are only possible in the mantle cavity of the host. Baker (1970a) studied the life cycle and off-host survival of *R. limacum*. Mites kept in culture cells survived for 8 days without food supply at room temperature. In our first experiment, parasite transmission occurred by mites that had temporarily left their host and stayed in the soil. It is, however, not known how long parasitic mites can survive in the soil. In our experiment, the intensity of the mite infection was higher in newly infected test snails compared to snails that transmitted the infection. Test snails might be more susceptible to mite infection because they were collected in a parasite-free population and thus were never exposed to *R. limacum*. However, the high intensity of the mite infection found in test snails suggests that several mites have been transmitted and that they successfully established a new parasite cohort.

Dissections of host snails revealed that the actual number of mites in the mantle cavity of *A. arbustorum* was about 10 times higher than the mite intensity estimated with the non-invasive method (Baur and Baur, 2005).

The hypothesis that mites of the genus *Riccardoella* follow mucus trails to locate host snails was first proposed by Turk and Phillips (1946) who observed that mites which temporarily left the host relocated them with high reliability. Our experiments provide evidence that *R. limacum* uses fresh mucus as a cue for their movements. Since individuals of *Riccardoella* are blind, visual orientation can be excluded as the interpretation of our findings (Fain and Van Goethem, 1986). Furthermore, as shown in Exp. 4, the preference for moving on fresh mucus is not an artefact caused by a different speed and/or directedness of mite movement. Most probably the chemical composition of mucus serves as a cue for *R. limacum*. Our experiment revealed a significant interaction between the substrate and the sequence of the treatment. The effect of the treatment was stronger when mites were first tested on slides containing fresh mucus. Mites removed from host snails and immediately tested may behave differently than mites that were temporarily stored on moist paper towel. Stress could partly explain this difference in locomotory behaviour.

Our experiments showed that the locomotion of *R. limacum* is influenced by the presence of fresh mucus. There was, however, no difference in the mite's movement behaviour on slides covered with dry mucus and on blank control slides. Mucus is widely used as a source of information among snails. Snails use mucus trails to locate mating partners and to discriminate between conspecific and heterospecific individuals (Shaheen *et al.* 2005). Parasites may also use cues from snail mucus. Our experiments were not designed to examine the importance of mucus-oriented mite locomotion in the field. It remains unclear on which spatial scale snail mucus is used to locate new hosts. However, our findings reject previous statements considering *R. limacum* as an exclusively sexually transmitted parasite.

Mechanisms of transmission strongly influence the interaction between the host and parasite populations (Fenton *et al.* 2002). Our results showed that *R. limacum* can be transmitted among hosts via soil. Furthermore, we demonstrated that *R. limacum* uses fresh mucus as a cue for locomotion. The findings support the hypothesis that *R. limacum* follows mucus trails to locate new hosts. The transmission of *R. limacum* via soil should be considered in commercial snail farming and when examining the epidemiology of wild snail populations.

We thank A. Baur and two anonymous referees for valuable comments on the manuscript. Financial support was received from the Swiss National Science Foundation (grant 31-110061).

REFERENCES

- Baker, R. A.** (1970a). Studies on the life history of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes). *Journal of Natural History* **4**, 511–519.
- Baker, R. A.** (1970b). The food of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes) and its relationship with pulmonate molluscs. *Journal of Natural History* **4**, 521–530.
- Barker, G. M.** (ed.) (2001). *The Biology of Terrestrial Molluscs*. CABI Publishing, Wallingford, Oxon., UK.
- Batschelet, E.** (1981). *Circular Statistics in Biology*, Academic Press, London.
- Baur, A. and Baur, B.** (1993). Daily movement patterns and dispersal in the land snail *Arianta arbustorum*. *Malacologia* **35**, 89–98.
- Baur, A. and Baur, B.** (2005). Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebrate Biology* **124**, 194–201. doi: 10.1111/j.1744-7410.2005.00019.x.
- Baur, B.** (1986). Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). *Holarctic Ecology* **9**, 117–125.
- Baur, B.** (1992). Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum* – experiments and an explanation. *Animal Behaviour* **43**, 511–518.
- Baur, B. and Raboud, C.** (1988). Life-history of the land snail *Arianta arbustorum* along an altitudinal gradient. *Journal of Animal Ecology* **57**, 71–87.
- Boots, M. and Meador, M.** (2007). Local interactions select for lower pathogen infectivity. *Science* **315**, 1284–1286. doi: 10.1126/science.1137126.
- Bull, J. J.** (1994). Virulence. *Evolution* **48**, 1423–1437.
- Combes, C.** (2001). *Parasitism: The Ecology and Evolution of Intimate Interactions*. The University of Chicago Press, Chicago, USA.
- Crossan, J., Paterson, S. and Fenton, A.** (2007). Host availability and the evolution of parasite life-history strategies. *Evolution* **61**, 675–684. doi: 10.1111/j.1558-5646.2007.00057.x.
- Ebert, D. and Herre, E. A.** (1996). The evolution of parasitic diseases. *Parasitology Today* **12**, 96–101.
- Fain, A. and Van Goethem, J. L.** (1986). Les acariens du genre *Riccardoella* Berlese, 1923 parasites du poumon de mollusques gastéropodes pulmonés terrestres. *Acarologia* **27**, 125–140.
- Fenton, A., Fairbairn, J. P., Norman, R. and Hudson, P. J.** (2002). Parasite transmission: reconciling theory and reality. *Journal of Animal Ecology* **71**, 893–905.
- Fenton, A. and Rands, S. A.** (2004). Optimal parasite infection strategies: a state-dependent approach. *International Journal for Parasitology* **34**, 813–821. doi: 10.1016/j.ijpara.2004.02.003.
- Frank, S. A. and Schmid-Hempel, P.** (2008). Mechanisms of pathogenesis and the evolution of parasite virulence. *Journal of Evolutionary Biology* **21**, 396–404. doi: 10.1111/j.1420-9101.2007.01480.x.
- Galvani, A. P.** (2003). Epidemiology meets evolutionary ecology. *Trends in Ecology & Evolution* **18**, 132–139.

- Ganusov, V. V. and Antia, R.** (2003). Trade-offs and the evolution of virulence of microparasites: do details matter? *Theoretical Population Biology* **64**, 211–220. doi: 10.1016/S0040-5809(03)00063-7.
- Graham, F. J.** (1994). The biology and control of *Riccardoella limacum* (Schrank), a mite pest of farmed snails. PhD thesis. University of Wales, UK.
- Graham, F. J., Ford, J. B. and Runham, N. W.** (1993). Comparison of two species of mites of the same genus, *Riccardoella* associated with Molluscs. *Acarologia* **34**, 143–148.
- Graham, F. J., Runham, N. W. and Ford, J. B.** (1996). Long-term effects of *Riccardoella limacum* living in the lung of *Helix aspersa*. *British Crop Protection Council Symposium Proceedings* **66**, 359–364.
- Hertel, J., Holweg, A., Haberl, B., Kalbe, M. and Haas, W.** (2006). Snail odour-clouds: spreading and contribution to the transmission success of *Trichobilharzia ocellata* (Trematoda, Digenea) miracidia. *Oecologia* **147**, 173–180. doi: 10.1007/s00442-005-0239-5.
- Kerney, M. and Cameron, R.** (1979). *A Field Guide to the Land Snails of Britain and North-west Europe*, Collins, London, UK.
- Krasnov, B. R., Khokhlova, I. S., Oguzoglu, I. and Burdelova, N. V.** (2002). Host discrimination by two desert fleas using an odour cue. *Animal Behaviour* **64**, 33–40. doi: 10.1006/anbe.2002.3030.
- Poulin, R.** (2007). *Evolutionary Ecology of Parasites*, 2nd Edn. Princeton University Press, Princeton, USA.
- R Development Core Team** (2008). *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing. URL <http://www.R-project.org>, Vienna, Austria.
- Rea, J. G. and Irwin, S. W. B.** (1994). The ecology of host-finding behaviour and parasite transmission – past and future perspectives. *Parasitology* **109**(Suppl.), S31–S39.
- Robb, T. and Forbes, M. R.** (2005). Success of ectoparasites: how important is timing of host contact? *Biology Letters* **1**, 118–120. doi: 10.1098/rsbl.2004.0271.
- Schüpbach, H. U. and Baur, B.** (2008). Parasitic mites influence fitness components of their host, the land snail *Arianta arbustorum*. *Invertebrate Biology* **127**, 350–356 doi:10.1111/j.1744-7410.2008.00138.x.
- Shaheen, N., Patel, K., Patel, P., Moore, M. and Harrington, M. A.** (2005). A predatory snail distinguishes between conspecific and heterospecific snails and trails based on chemical cues in slime. *Animal Behaviour* **70**, 1067–1077. doi: 10.1016/j.anbehav.2005.02.017
- Turk, F. A. and Phillips, S. M.** (1946). A monograph of the slug mite – *Riccardoella limacum* (Schrank). *Proceedings of the Zoological Society of London* **115**, 448–472.

CHAPTER 4

Contact-based transmission models in terrestrial gastropod populations infected with parasitic mites

Hans Ulrich Schüpbach and Bruno Baur

International Journal for Parasitology (2010), in press

Contact-based transmission models in terrestrial gastropod populations infected with parasitic mites

H. U. Schüpbach and B. Baur, Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johannis-Vorstadt 10, CH-4056 Basel, Switzerland.

Original Research Paper

Corresponding author

Hans Ulrich Schüpbach, Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johannis-Vorstadt 10, CH-4056 Basel, Switzerland.

Tel. +41 61 267 08 44, Fax +41 61 267 08 32, e-mail: H.Schuepbach@unibas.ch

Abstract

Parasite transmission fundamentally affects the epidemiology of host-parasite systems, and is considered to be a key element in the epidemiological modelling of infectious diseases. Recent research stressed the importance of detailed disease-specific variables involved in the transmission process. *Riccardoella limacum* is a hematophagous mite living in the mantel cavity of terrestrial gastropods. In this study, we experimentally examined whether the transmission success of *R. limacum* is affected by the contact frequency, parasite load and/or behaviour of the land snail *Arianta arbustorum*, a common host of *R. limacum*. In the experiment the transmission success was mainly affected by physical contacts among snails and slightly influenced by parasite intensity of the infected snail. Using these results we developed two different transmission models based on contact frequencies and transmission probability among host snails. To parameterize the models we used life-history data from three natural *A. arbustorum* populations with different population densities. Data on contact frequencies of video-recorded snail groups were used to fit the density response of the contact function, assuming either a linear relationship (model 1) or a second-degree polynomial relationship based on the ideal gas model of animal encounter (model 2). We calculated transmission coefficients (β), basic reproductive ratios (R_0) and host threshold population densities for parasite persistence in the three *A. arbustorum* populations. We found higher transmission coefficients (β) and larger R_0 -values in model 1 than in model 2. Furthermore, the host population with the highest density showed larger R_0 -values (16.47–22.59) compared to populations with intermediate (2.72–7.45) or low population density (0.75–4.10). Host threshold population density for parasite persistence ranged from 0.35 to 2.72 snails per m². Our results show that the integration of the disease-relevant biology of the organisms concerned may improve models of host-parasite dynamics.

Key words: Parasite transmission; epidemiology; basic reproductive ratio; transmission model; *Riccardoella limacum*; *Arianta arbustorum*

1. Introduction

The transmission process is one of the major forces influencing the epidemiology of host-parasite systems (Fenton et al., 2002; Galvani, 2003). The localisation and successful infection of new hosts are essential for the parasite's fitness and may directly affect the life-history and demography of the host population (Minchella and Scott, 1991; Agnew et al., 2000). Attributes of the transmission process strongly differ both among hosts and among parasites. The population density of hosts (Greer et al., 2008), contact rate among hosts (Balenghien et al., 2005) and host behaviour (Ryder et al., 2007; Greer and Collins, 2008) as well as the mode of transmission (Clayton and Tompkins, 1994), the dose of transmitted parasites (Ben-Ami et al., 2008) and their infectivity (Bull, 1994) may lead to pronounced differences in the epidemiology of the interacting species (Fenton et al., 2002; Ganusov and Antia, 2003; Frank and Schmid-Hempel, 2008). In epidemiological models, parasite transmission is generally expressed by the transmission coefficient (β), which specifies the rate at which parasites are transmitted among infected and susceptible hosts. Since transmission coefficients are highly disease-specific, the decomposition of the transmission term into disease-specific aspects of the transmission process may enhance the accuracy and strongly increase the quality of epidemiological models (Begon et al., 2002; Real and Biek, 2007; Antolin, 2008). Furthermore, this approach may improve the assessment of important disease-specific terms including the basic reproductive ratio (R_0), which is defined as the expected number of secondary infections originating from an infected individual introduced into a susceptible population (Heesterbeek, 2002; Heffernan et al., 2005).

Many macroparasite species are actively transmitted among host individuals during host contact or through mobile, free-living stages of the parasite (Combes, 2001). The contact structure is playing a major role in the epidemiology of directly transmitted diseases (Kiss et al., 2009). Parasite transmission may be higher in dense populations, in large social groups and in species with promiscuous mating systems (Altizer et al., 2003). The mite *Riccardoella limacum* is a hematophagous ectoparasite of land snails (Fain and van Goethem, 1986). The parasite feeds and reproduces in the mantle cavity of their host

species. Heavy infestation with *R. limacum* reduces the growth rate and delays reproductive development in the snail *Cornu aspersum*, and can seriously affect the economy of commercial snail farming (Graham, 1994; Graham et al., 1996). In the host snail *Arianta arbustorum*, the mite is actively transmitted during courtship and mating. Furthermore, mites are transmitted via soil from infested to parasite-free hosts (Schüpbach and Baur, 2008a). Hence, the transmission of *R. limacum* may be influenced by the frequency of body contacts between susceptible and infected individuals, the parasite intensity of infected hosts and by the behaviour of host snails encountering conspecifics.

The aim of our study was to use experimental data on the transmission process of a macroparasite to elucidate the epidemiology of natural populations and to predict the performance of host and parasite under natural conditions. For this purpose, we experimentally examined whether mite transmission in *A. arbustorum* is affected by (1) the number of encounters between parasite-free and mite-infected snails, (2) the parasite intensity of a particular snail, and (3) host behaviour (i.e. snail activity and the number of physical contacts between different snails). We manipulated encounter frequency by keeping pairs consisting of a parasite-free and a mite-infected snail in the same container for different periods of time. Parasite intensity of the mite-infected snail was considered as a co-variable. Using the results of this experiment, we parameterized epidemiological models based on contact frequencies of host snails and transmission probabilities between parasitized and parasite-free snails (Begon et al., 2002; Real and Biek, 2007). The contact function (i.e. the number of host contacts in relation to population density) was modelled with data on contact frequencies from video recorded behaviour of snail groups assessed in a separate experiment. We used the probability of successful transmission during snail contact and data from three mite-infected snail populations in the wild (population density, parasite prevalence and snail mortality) to calculate transmission coefficients, basic reproductive rates (R_0) and threshold host densities for parasite persistence (N_T) of *R. limacum* in *A. arbustorum* populations (McCallum et al., 2001).

2. Materials and methods

2.1. Study species

Riccardoella limacum is a parasitic mite that lives in the mantle cavity of land snails (Fain and van Goethem, 1986). The parasite's life cycle has been studied under laboratory conditions in the host snail *Cornu aspersum* (Graham, 1994). Female mites lay their eggs in the respiratory tissue of their host. Three nymphal mite stages are followed by sexually mature males and females, both 0.4 mm in body length (Baker, 1970b). The total life cycle of *R. limacum* lasts 19–23 d at temperatures of 20°–25° C. *R. limacum* is a blood-sucking parasite (Baker, 1970a), which causes considerable harm in *C. aspersum* by reducing the activity and growth rate and by delaying reproductive development (Graham et al., 1996).

Arianta arbustorum, a common host of *R. limacum*, is a simultaneously hermaphroditic helioid land snail common in moist habitats of northwestern and central Europe (Kerney and Cameron, 1979). Individuals become sexually mature at an age of 2–4 years and live for another 3–4 years (Baur and Raboud, 1988). The snail usually reproduces through outcrossing (Kupfernagel et al., 2010). Mating includes elaborate courtship and lasts 2–18 hours (Baur, 1992). A considerable variation in prevalence and intensity of *R. limacum* infection was found in wild *A. arbustorum* populations in Switzerland (Baur and Baur, 2005). The parasite occurred in 4 out of 11 populations examined with a prevalence of 45.8–77.8%. Mite-infection affects life-history and behaviour of *A. arbustorum*. Infected hosts laid fewer eggs and were less active. Furthermore, in two out of three populations and in experimentally infected snails, hosts suffered an increased mortality during hibernation compared to uninfected snails (Schüpbach and Baur, 2008b).

Transmission of *R. limacum* mainly occurs during the long-lasting courtship and mating of host snails. Individuals of *R. limacum* move from infected hosts to their mating partners (H.U. Schüpbach, personal observation). Transmission does not occur among snails kept isolated in the laboratory. However, mite transmission also occurs indirectly via soil (Schüpbach and Baur, 2008a). In laboratory experiments, mites were transmitted

without physical contact from mite-infected to parasite-free snails. *Riccardoella limacum* showed a preference to move on fresh snail mucus and might use fresh mucus as a cue to locate new hosts. However, it is unknown to what extent the different routes of transmission contribute to the actual transmission of *R. limacum* in wild populations of *A. arbustorum*.

2.2. Experimental parasite transmission

We randomly collected parasite-free snails (hereafter referred to as test snails) in a mite-free population in the subalpine forest near Gurnigelbad, 30 km south of Bern, Switzerland (46°45'N, 7°27'E; elevation 1330 m). Mite-infected snails were collected in Nuglar (47°29' N, 7°42' E; elevation 430 m). The snails were kept individually in transparent plastic beakers (6.5 cm in diameter, 8 cm deep) on moist soil mixed with powdered limestone under a light : dark regime of 16 : 8 h and a constant temperature of $19^{\circ} \pm 1^{\circ}$ C. The soil was obtained from the locality Gurnigelbad where *R. limacum* does not occur (Baur and Baur, 2005). The beakers were cleaned 1–2 times per week to remove feces and fresh lettuce was provided *ad libitum* as food. The infection status and the intensity of infection of the host snails were assessed using a non-invasive screening method (Baur and Baur, 2005). The soft body and respiratory pore of each individual were carefully examined for mites using a magnifying glass (10x). Mite screening was repeated three times on different days. A snail was considered as parasite-infected if at least one mite could be detected in three observations. The intensity of infection was expressed as mean number of mites averaged across the three examinations (Baur and Baur, 2005). Previous analyses revealed a high repeatability of this method (92.9%; Baur and Baur 2005). Furthermore, visual mite-assessment corresponded with the parasite record of dissected snails: 87.5% of mite-infected snails were correctly assigned either as being infected or uninfected by the non-invasive method (Baur and Baur, 2005).

We investigated the effects of encounter frequency, intensity of infection and behaviour of infected snails on the transmission success of *R. limacum* to uninfected snails. We manipulated encounter frequency by keeping pairs of snails each consisting of a test individual and a mite-infected individual for different periods of time in plastic

beakers. In total, we tested 62 snail pairs. Each snail pair was placed in a separate plastic beaker (6.5 cm in diameter, 8 cm deep) lined with moist, parasite-free soil. In treatment 1, pairs of infected and uninfected snails ($n = 21$) were kept together for 3 h. In treatment 2, pairs ($n = 21$) were kept together two times for 3 h (total 6 h), and in treatment 3 ($n = 20$) four times for 3 h (total 12 h). The experiment was run at night. The recurring trials in treatment 2 and 3 were run in subsequent nights using the same pairs of snails. After the experimental procedure each snail was kept in its original beaker. The parasite intensity of the mite-infected snails, which ranged from low (0.33 mites) to high (12 mites) with a mean of 2.48 ± 0.40 mites ($n = 62$), was considered as a co-variable. With respect to mite intensity, we assigned the snails to the treatments in such a way that the mean parasite intensity was equal in all three treatments ($\chi^2 = 0.149$, $df = 2$, $P = 0.93$). Transmission opportunity may be related to host activity. We therefore assessed the behaviour of the snails during the trials by recording their activity every 15 minutes. We classified the activity of each snail using a four-graded scale (1 = soft body retracted; 2 = soft body extended but tentacles retracted; 3 = soft body and tentacles extended; 4 = crawling). The overall activity of a snail was expressed as the cumulative percentage of records of an individual in the activity classes 2, 3 and 4. We also recorded the number of physical contacts between test snails and infected snail in each snail pair and calculated the probability of parasite transmission per host contact (v). Six weeks after the experiment (two mite generations; Graham et al., 1996), we examined the transmission success of *R. limacum* by assessing the infection status and the intensity of mite infection in test snails using the non-invasive screening method (described above).

Statistical analysis. Data analysis was performed using R Statistical Software (R Development Core Team, 2008). Generalized linear models (logistic ANOVA with binomial errors and logit link function) and chi-square tests were used to examine the influence of treatment, parasite intensity and snail behaviour (snail activity and the number of physical contacts among snails) on the transmission success of *R. limacum*. Means \pm SE are reported.

2.3. Epidemiological models

Transmission models were developed by combining data on contact patterns of *A. arbustorum* and transmission probabilities of *R. limacum* (Begon et al., 2002; Real and Biek, 2007). Based on SI-models (Anderson and May, 1979; McCallum et al., 2001), we first calculated transmission coefficients using a contact function derived from the frequency of contacts of video-recorded snail groups (see below). We then used data from three wild *A. arbustorum* populations infected with *R. limacum* to calculate basic reproductive ratios (R_0) and threshold host population densities (N_T) for parasite persistence in each population.

Contact function. The contact function describes how the frequency of contacts among individuals in a population is related to the population density. We used data on contact frequencies from video recorded behaviour of uninfected snail groups to calculate the contact function of *A. arbustorum*. Six snails were kept together in transparent plastic boxes (29 x 19 x 17 cm) lined with moist soil over a period of 58 days, covering the maximum mating activity in natural snail populations in which transmission of *R. limacum* may occur. This set-up was replicated six times with different snail groups. To record the snail behaviour, time-lapse photography with a frame interval of 2 min was used. The number of contacts among snail individuals was assessed by evaluating the videotapes with the software PictViewer. This software was used to determine the exact position of snail individuals in the container at intervals of 4 sec and to record the physical contacts between snails. An encounter that lasts more than 4 minutes was defined as a contact between two individuals. The threshold of 4 minutes allowed us to exclude apparent encounters of moving snails, which did not interact physically. We used the total number of contacts for each snail in the six containers ($n = 36$ snails) to calculate the mean number of contacts.

Based on the contact pattern of the video-recorded snails, we defined the contact function in two different ways. In model 1, we assumed a linear increase of the contact frequency with increasing population density, whereas in model 2, we assumed a contact pattern that corresponds to the ideal gas model of animal encounter (Hutchinson and

Waser, 2007). In model 1, we used data of the video-recorded contact frequencies to fit a regression line. We then defined κ as the first derivative of the linear contact function. In model 2, animal encounter frequencies were modelled in a two-dimensional plane based on the mathematical formulation of encounter frequencies of gas molecules (Hutchinson and Waser, 2007). The number of contacts (c) of individuals moving with a constant velocity (v) in a two-dimensional area (A) is expressed as $c = 4\rho^2ADvt/\pi$. The variable ρ specifies the detection distance of two individuals. Based on the morphology of moving snails we set ρ as 1 cm. We first calculated the mean velocity of snails from the video recorded survey of the snail groups as $v = c\pi/4\rho^2ADt$. Then we fitted a 2nd order polynomial to the contact function and defined κ as the first derivative of the contact function.

Transmission models. The transmission coefficient (β) is the rate at which susceptible hosts are converted into infected hosts and is defined as the constant of proportionality of the transmission function (i.e. the function describes the transmission rate in relation to the density of the host population; McCallum et al., 2001). In our models β was expressed as κv , the product of the slope of the contact function (κ) and the probability of parasite transmission during a contact between an infected and a susceptible host (v ; see experimental parasite transmission) (Begon et al., 2002). The spread of a disease in a host population largely depends on the reproductive ratio (R_0), which is the expected number of secondary infections originating from an infected individual introduced into a susceptible population (Heesterbeek, 2002). We calculated R_0 according to McCallum et al. (2001) as $R_0 = \beta * D / (\alpha + b)$, where D is the population density, α is the parasite induced hibernation mortality and b is the natural mortality during the reproductive season. Accordingly, the effective reproductive ratio (R) was calculated by dividing R_0 by the parasite prevalence (McCallum et al., 2001). The threshold population density of the host for parasite persistence was expressed as $N_T = (\alpha + b) / \beta$. This term specifies the minimal population density at which a parasite can persist in a population (Deredec and Courchamp, 2003).

Parameterisation of transmission models. We used data on population densities, parasite prevalence, and mortality during hibernation of mite-infected and parasite-free snails of three mite infected snail populations in Switzerland (Schüpbach and Baur, 2008b). In each population (Weissenstein: 47°15'N, 7°29'E; elevation 1230 m; Nuglar: 47°29'N, 7°42'E; 430 m; Thun: 46°44'N, 7°35'E; 580 m) a sample of adult snails was collected, screened for parasite infection (as described above) and allowed to hibernate under conditions similar to those in the field (for details see Schüpbach and Baur, 2008b). We assessed the prevalence of parasite infection (proportion of infected individuals in a population) and the mortality during hibernation for parasite-infected and parasite-free snails.

Data on the background mortality of *A. arbustorum* during the reproductive season were obtained from a survey of four snail populations (60 snails per population; Baur and Raboud, 1988). In each population, mortality was recorded in six age classes of adult snails during one reproductive season (for details see Baur and Raboud, 1988). We used the mean mortality during the reproductive season of the four snail populations.

Model assumptions. We assume that infected and susceptible hosts mix completely with each other and move randomly within an area of fixed size. Furthermore, we assume that hosts do not differ in their susceptibility to parasite infection and that clearance of the infection does not occur. Although there is increasing evidence that the innate immune reaction in invertebrates is highly specific to different pathogens (Humphries and Yoshino, 2003; Kurtz, 2005; Coustau, 2009), it is largely unknown how invertebrates defend themselves against ectoparasites. We also assume that parasite-induced mortality occurs during hibernation or shortly afterwards (as recorded in Schüpbach and Baur, 2008b).

3. Results

3.1. Experimental parasite transmission

Parasitic *R. limacum* were transmitted in 10 out of 62 snail pairs (16.1%) tested. Six weeks after the experiment the mean parasite intensity of the infected test snails ($n = 10$)

was 3.03 ± 1.03 mites. The mite intensity of test snails (i.e. previous uninfected snails) and that of infected test partners were not correlated (Pearson's correlation: $r = 0.30$; $n = 10$; $P = 0.396$).

Considering the three treatment groups separately, mites were transmitted in one out of 21 pairs (4.8%) with snails kept 3 h together, in four out of 21 pairs (19.1%) with snails kept 6 h together, and in 5 out of 20 pairs (25.0%) with snails kept 12 h together. However, the difference in transmission success among the three treatment groups was not significant ($\chi^2 = 3.80$, $df = 2$, $P = 0.150$).

Physical contact between test snails and infected snails was observed in 27 out of the 62 pairs (43.6%). Eight out of 10 newly infected snails had contact with their infected partner, whereas in two newly infected snails no contact was observed. Transmission success of *R. limacum* tended to increase with increasing parasite intensity (generalized linear model; $\chi^2 = 3.49$; $df = 1$; $P = 0.062$), and was higher in pairs in which physical contact was observed during the experiment ($\chi^2 = 7.62$, $df = 1$; $P = 0.006$). However, transmission success did not increase with increasing number of contacts ($\chi^2 = 1.56$; $df = 1$; $P = 0.119$). Snail activity did not affect the transmission of *R. limacum*. Neither the activity of the test snail ($\chi^2 = 0.10$, $df = 1$, $P = 0.747$) nor the activity of the parasite-infected snail ($\chi^2 = 0.32$, $df = 1$, $P = 0.571$) affected the transmission success of *R. limacum*. The overall activity did not differ between infected and parasite free snails ($\chi^2 = 0.121$; $df = 1$; $P = 0.73$). The probability of successful transmission among snail pairs (v) was 0.37 (*R. limacum* was transmitted in 10 of the 27 snail pairs).

3.2. Epidemiological models

Contact function. Six replicates of snail groups consisting of six individuals were observed over a period of 58 days. The number of contacts averaged 84.83 ± 7.04 S.E. per snail ($n = 36$) within 58 days. The surface of each plastic box covered an area of 0.2734 m^2 (including walls and cover). Snail density was 21.87 individuals per m^2 box surface, which is within the range of snail densities observed in natural populations (Baur, 1986). In model 1, the number of contacts increased linearly, leading to the contact function $f(x) = 3.87x$, with a slope of $\kappa = f'(x) = 3.87$. In model 2, the mean velocity (v)

in the six snail groups was $1.01 \times 10^{-5} \text{ms}^{-1}$, leading to the contact function $f(x) = -163.84 + 10.74x + 0.18(x-30.5)^2$, assuming an ideal gas model of animal encounter. The slope of this contact function was $\kappa = f'(x) = 10.74 + 0.36(x-30.5)$.

Parameterisation of transmission models. Snail populations differed in local density, prevalence of mite infection and survival during hibernation. Considering the range of densities recorded in natural *A. arbustorum* populations (Baur, 1986, 1988), the density of the Nuglar population was relatively high (8 snails per m^2), moderately high in the Thun population (4 snails per m^2) and low in the Weissenstein population (2 snails per m^2 ; Table 1). Furthermore, the prevalence of mite infection and the winter mortality differed among snail populations (Table 1). Winter mortality of mite-infected snails was lower in the Nuglar population (0.13) compared to the Weissenstein (0.32) and Thun population (0.39; $\chi^2 = 20.42$; $df = 1$; $P < 0.0001$). Furthermore, mortality during the reproductive season was assumed to be 0.38, which corresponds to the mean mortality of four snail populations over one reproductive season (Baur and Raboud, 1988).

Transmission models. In model 1, the transmission coefficient (β) of the three snail populations was 1.43. β did not differ among snail populations because the slope of the contact function is constant in this model. In model 2, β was 1.04 in the Nuglar population, 0.26 in the Weissenstein population and 0.52 in the Thun population. Thus, the transmission coefficient was higher under the assumptions of model 1 (Table 2).

The basic reproductive ratio (R_0) increased with increasing population density and thus differed among snail populations (Table 2). R_0 -values were larger in model 1 (range of $R_0 = 4.10 - 22.59$) than in model 2 ($R_0 = 0.75 - 16.47$; Table 2). The effective reproductive ratios (R ; i.e. the expected number of resulted infections in the respective population per infected individual) were higher in model 1 than in model 2. However, R was much higher in the Nuglar population (range: 6.59 – 9.04; Table 2) than in the Weissenstein and Thun populations (range: 0.41 – 2.26). Since R is smaller than 1, parasite prevalence would temporarily decrease in the Weissenstein and Thun population.

Threshold population densities for parasite persistence ranged from 0.35 snails per m^2 (Nuglar population; model 1) up to 2.72 snails per m^2 (Weissenstein population; model

2). The critical population size at the three localities ranged from 0.35 to 0.54 snails per m^2 in model 1 and from 0.49 to 2.72 snails per m^2 in model 2.

4. Discussion

The results of this study showed that contact based transmission models are a helpful tool to model the epidemiological dynamics of ectoparasites in natural host populations. Furthermore, we showed that the integration of the disease-relevant parameters allowed a prediction of the infection dynamics of different host populations. Transmission of *R. limacum* between parasite-infected and parasite-free *A. arbustorum* occurred in pairs with physical contacts, and tended to be affected by parasite intensity of the infected snail. These findings suggest that parasite transmission mainly occurs during encounters of snail individuals. Transmission by free-living mites on soil may also occur (Schüpbach and Baur, 2008a), but might not be the conventional transmission route in *R. limacum*. Contact networks are a key factor in the transmission of directly transmitted parasites. Increased network connectivity may increase the risk of acquiring an infection (Otterstatter and Thomson, 2007; Godfrey et al., 2009). Contact patterns are highly heterogeneous in most species, violating the assumption of random mixing, on which mathematical models are based (Perkins et al., 2008). In *A. arbustorum* encounters among adult individuals may most frequently occur during the long-lasting courtship and mating (Baur, 1992). Mating frequency in *A. arbustorum* has been shown to increase with increasing population density (Kupfernagel et al., 2010). Transmission may also occur during incidental encounters not related to mating activity, and in snails resting in clumped patterns on single plants (Baur, 1986) and thus also infecting juvenile individuals (Baur and Baur, 2005). In contrast to social host species, contact patterns in *A. arbustorum* may be closely related to population density.

The shape of density-dependent transmission functions strongly differs among hosts and among parasites (Ganusov and Antia, 2003) and may considerably affect the dynamics of host-parasite systems (Hochberg, 1991). Empirical quantification of the transmission function revealed that a linear response of transmission rate to population density is often violated in host-parasite systems (Fenton et al., 2002). In our models, we

either assumed a linear (model 1) or a second-order polynomial contact function (model 2), and fitted the functions with data from video-recorded behaviour of snail groups kept in the laboratory. In the wild, factors such as habitat structure, prevailing weather conditions and predation may influence the snails' movement pattern. The quality of epidemiological models based on contact pattern among host individuals could be improved by incorporating transmission functions assessed under field conditions (Real and Biek, 2007; Schaubert et al., 2007). We assessed the contact function using uninfected *A. arbustorum*. Locomotion and the resulting contact patterns might differ both between infected and uninfected snails and among populations.

The basic reproductive ratio (R_0) is frequently used as a threshold parameter to predict the dynamics of pathogens in host populations. A disease may spread in a susceptible population if $R_0 > 1$ (Heffernan et al., 2005). Basic reproductive ratios obtained in our models revealed a high variation among snail populations and predict a rapid spread of *R. limacum* introduced in susceptible host populations. Considering the effective reproductive ratio (R), in two out of three *A. arbustorum* populations R is smaller than 1 in model 2, which would predict a temporary decline in the parasite prevalence. This result suggests that R and R_0 might be underestimated in model 2.

Basic and effective reproductive ratios were larger in the Nuglar population than in the Weissenstein and Thun population. Such a large R implies a higher parasite prevalence than recorded in the Nuglar population. Several mechanisms might explain the relative low parasite prevalence in the high-density population Nuglar. First, the density-dependent contact function might level off under high densities as a result of interference competition by mucus trails (Baur, 1988), leading to a reduced transmission in high-density snail populations. In many host-parasite systems the transmission functions decrease in response to increasing densities (Fenton et al., 2002). Second, in contrast to our model assumptions, parasite resistance and/or the clearance rate might be higher in the Nuglar population than in the Weissenstein and Thun populations. Our assumption that clearance of the infection and resistance to the infection do not occur is based on data from experimentally infected *A. arbustorum* kept under laboratory conditions. Mite infection was successful in 96.5% of the snails infected and clearance of the infection

could not be observed (H.U. Schüpbach, unpublished data). Third, it is possible that the Nuglar population deviated from the epidemiological equilibrium and parasite prevalence increased in the course of the survey. However, parasite prevalence, which was repeatedly assessed in the Nuglar population, was consistent over time.

Our models predict that the occurrence of *R. limacum* is impeded in host populations with densities below 0.35 – 2.72 snails per m². In fact, a survey of 11 *A. arbustorum* populations revealed that *R. limacum* is not consistently distributed in host populations in Switzerland. *Riccardoella limacum* occurred in 36.4% of the populations examined (Baur and Baur, 2005). Besides host threshold population densities, the distribution of *R. limacum* might be limited by climatic conditions. *Riccardoella limacum* did not occur in alpine *A. arbustorum* populations. The survival of mite eggs in the pulmonary cavity of the host might decrease due to the extended period of snail hibernation at high altitudes (Baur and Baur, 2005).

In this study we parameterised epidemiological models, which are based on experimental investigation of the transmission process of an invertebrate host-ectoparasite system. Our findings suggest that a linear contact function (model 1) may promote a better prediction of snail encounters in the wild than model 2. Although daily movement patterns of *A. arbustorum* are random with respect to direction and distance (Baur and Baur, 1992), model 2 may underestimate the contact network of *A. arbustorum* in low-density populations. Our results show that the incorporation of the disease-relevant biology of the organisms concerned may help to improve the models of host-parasite dynamics. Since the transmission process strongly differs among host-parasite systems (Fenton et al., 2002), an organism-specific adjustment of the model parameter may be required in order to meet the life history of the organisms involved. Furthermore, such models may be essential to predict the course of parasite infections in host populations.

Acknowledgements

We thank O. Müller and A. Wirth for laboratory assistance and H.P. Rusterholz for statistical advice. A. Baur and P. Stoll and two anonymous reviewers provided valuable

comments on the manuscript. Financial support was received from the Swiss National Science Foundation.

References

- Agnew, P., Koella, J.C., Michalakis, Y., 2000. Host life history responses to parasitism. *Microb. Infect.* 2, 891-896.
- Altizer, S., Nunn C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pedersen, A.B., Poss, M., Pulliam, J.R.C., 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annu. Rev. Ecol. Evol. Syst.* 34, 517-547.
- Anderson, R.M., May, R.M., 1979. Population biology of infectious diseases 1. *Nature* 280, 361-367.
- Baker, R.A., 1970a. The food of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes) and its relationship with pulmonate molluscs. *J. Nat. Hist.* 4, 521-530.
- Baker, R.A., 1970b. Studies on the life history of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes). *J. Nat. Hist.* 4, 511-519.
- Balenghien, T., Chalvet-Monfray, K., Bicout, D.J., Sabatier, P., 2005. Modelling and determination of the transmission contact rate for contagious bovine pleuropneumonia. *Epidemiol. Infect.* 133, 337-342.
- Baur, A., Baur, B., 1992. Effect of corridor width on animal dispersal - a simulation study. *Glob. Ecol. Biogeogr. Lett.* 2, 52-56.
- Baur, A., Baur, B., 1993. Daily movement patterns and dispersal in the land snail *Arianta arbustorum*. *Malacologia* 35, 89-98.
- Baur, A., Baur, B., 2005. Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebr. Biol.* 124, 194-201.
- Baur, B., 1986. Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). *Holarctic Ecol.* 9, 117-125.

- Baur, B., 1988. Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. *Oecologia* 77, 390-394.
- Baur, B., 1992. Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum* – experiments and an explanation. *Anim. Behav.* 43, 511-518.
- Baur, B., Raboud, C., 1988. Life-history of the land snail *Arianta arbustorum* along an altitudinal gradient. *J. Anim. Ecol.* 57, 71-87.
- Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M., Turner, J., 2002. A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiol. Infect.* 129, 147-153.
- Ben-Ami, F., Regoes, R.R., Ebert, D., 2008. A quantitative test of the relationship between parasite dose and infection probability across different host-parasite combinations. *Proc. R. Soc. B* 275, 853-859.
- Bull, J.J., 1994. Virulence. *Evolution* 48, 1423-1437.
- Clayton, D.H., Tompkins, D.M., 1994. Ectoparasite virulence is linked to mode of transmission. *Proc. R. Soc. B* 256, 211-217.
- Combes, C., 2001. *Parasitism: The Ecology and Evolution of Intimate Interactions*. The University of Chicago Press, Chicago.
- Coustau, C., 2009. Immunity in parasite-vector snails. *M S-Med. Sci.* 25, 399-403.
- Deredec, A., Courchamp, F., 2003. Extinction thresholds in host-parasite dynamics. *Ann. Zool. Fenn.* 40, 115-130.
- Fain, A., van Goethem, J.L., 1986. Les acariens du genre *Riccardoella* Berlese, 1923 parasites du poumon de mollusques gastéropodes pulmonés terrestres. *Acarologia* 27, 125-140.
- Fenton, A., Fairbairn, J.P., Norman, R., Hudson, P.J., 2002. Parasite transmission: reconciling theory and reality. *J. Anim. Ecol.* 71, 893-905.
- Frank, S.A., Schmid-Hempel, P., 2008. Mechanisms of pathogenesis and the evolution of parasite virulence. *J. Evol. Biol.* 21, 396-404.
- Galvani, A.P., 2003. Epidemiology meets evolutionary ecology. *Trends Ecol. Evol.* 18, 132-139.

- Ganusov, V.V., Antia, R., 2003. Trade-offs and the evolution of virulence of microparasites: do details matter? *Theor. Popul. Biol.* 64, 211-220.
- Godfrey, S.S., Bull, C.M., James, R., Murray, K., 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behav. Ecol. Sociobiol.* 63, 1045-1056.
- Graham, F., 1994. The biology and control of *Riccardoella limacum* (Schrank), a mite pest of farmed snails. PhD dissertation, University of Wales.
- Graham, F.J., Runham, N.W., Ford, J.B., 1996. Long-term effects of *Riccardoella limacum* living in the lung of *Helix aspersa*. *BCPC Symposium Proceedings* 66, 359-364.
- Greer, A.L., Briggs, C.J., Collins, J.P., 2008. Testing a key assumption of host-pathogen theory: density and disease transmission. *Oikos* 117, 1667-1673.
- Greer, A.L., Collins, J.P., 2008. Habitat fragmentation as a result of biotic and abiotic factors controls pathogen transmission throughout a host population. *J. Anim. Ecol.* 77, 364-369.
- Heesterbeek, J.A.P., 2002. A brief history of R_0 and a recipe for its calculation. *Acta Biotheor.* 50, 375-376.
- Heffernan, J.M., Smith, R.J., Wahl, L.M., 2005. Perspectives on the basic reproductive ratio. *J. R. Soc. Interface* 2, 281-293.
- Hochberg, M.E., 1991. Population dynamic consequences of the interplay between parasitism and intraspecific competition for host-parasite systems. *Oikos* 61, 297-306.
- Humphries, J.E., Yoshino, T.P., 2003. Cellular receptors and signal transduction in molluscan hemocytes: Connections with the innate immune system of vertebrates. *Integr. Comp. Biol.* 43, 305-312.
- Hutchinson, J.M.C., Waser, P.M., 2007. Use, misuse and extensions of "ideal gas" models of animal encounter. *Biol. Rev.* 82, 335-359.
- Kerney, M., Cameron, R., 1979. *A Field Guide to the Land Snails of Britain and North-West Europe*. Collins, London.
- Kiss, I.Z., Simon, P.L., Kao, R.R., 2009. A contact-network-based formulation of a preferential mixing model. *B. Math. Biol.* 71, 888-905.

- Kupfernagel, S., Rusterholz, H.P., Baur, B., 2010. Variation in multiple paternity and sperm utilization patterns in natural populations of a simultaneous hermaphrodite land snail. *Biol. J. Linn. Soc.* 99, 350-361.
- Kurtz, J., 2005. Specific memory within innate immune systems. *Trends Immunol.* 26, 186-192.
- McCallum, H., Barlow, N., Hone, J., 2001. How should pathogen transmission be modelled? *Trends Ecol. Evol.* 16, 295-300.
- Minchella, D.J., Scott, M.E., 1991. Parasitism – a cryptic determinant of animal community structure. *Trends Ecol. Evol.* 6, 250-254.
- Otterstatter, M.C., Thomson, J.D., 2007. Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia* 154, 411-421.
- Perkins, S.E., Ferrari, M.F., Hudson, P.J. 2008. The effects of social structure and sex-based transmission on macroparasite infection. *Parasitology* 135, 1561-1569.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. URL <http://www.R-project.org>, Vienna, Austria.
- Real, L.A., Biek, R., 2007. Infectious disease modeling and the dynamics of transmission. *Wildlife and emerging zoonotic diseases: the biology, circumstances and consequences of cross-species transmission.* *Curr. Topics Microbiol. Immunol.* 315, 33-49.
- Ryder, J.J., Miller, M.R., White, A., Knell, R.J., Boots, M., 2007. Host-parasite population dynamics under combined frequency- and density-dependent transmission. *Oikos* 116, 2017-2026.
- Schauber, E.M., Storm, D.J., Nielsen, C.K., 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. *J. Wildlife Manage.* 71, 155-163.
- Schüpbach, H.U., Baur, B., 2008a. Experimental evidence for a new transmission route in a parasitic mite and its mucus-dependent orientation towards the host snail. *Parasitology* 135, 1679-1684.

Schüpbach, H.U., Baur, B., 2008b. Parasitic mites influence fitness components of their host, the land snail *Arianta arbustorum*. *Invertebr. Biol.* 127, 350-356.

Table 1. Parameters used in the transmission models: population density, parasite prevalence and winter mortality in three mite-infected *A. arbustorum* populations in Switzerland. Mortality during the reproductive season was assessed in other parasite-free populations.

Parameter	Abbr.	Snail population			Data source
		Nuglar	Weissenstein	Thun	
Population density (adults / m ²)	D	8	2	4	Schüpbach and Baur (2008b)
Prevalence of parasitic mites	I	0.60	0.45	0.71	Schüpbach and Baur (2008b)
Winter mortality of infected snails	α	0.127	0.319	0.389	Schüpbach and Baur (2008b)
Mortality during reproductive season	b	0.380	0.380	0.380	Baur and Raboud (1988)

Table 2. Transmission coefficient, basic and effective reproductive ratio and threshold population densities for parasite persistence in three *Arianta arbustorum* populations infected with *Riccardoella limacum*. The coefficients were calculated using transmission models based on contact frequencies of *A. arbustorum*. Model 1 is based on a linear contact function and in model 2 the contact function follows the ideal gas model of animal encounter.

Parameter	Abbr.	Snail population					
		Nuglar		Weissenstein		Thun	
		Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
Transmission coefficient	β	1.43	1.04	1.43	0.26	1.43	0.52
Basic reproductive ratio	R_0	22.59	16.47	4.10	0.75	7.45	2.72
Effective reproductive ratio	R	9.04	6.59	2.26	0.412	2.16	0.79
Threshold population density for parasite persistence	N_T	0.35	0.63	0.49	2.72	0.54	1.47

GENERAL DISCUSSION

Parasite-induced impact on host life-history and parasite transmission among host individuals are important determinants of the epidemiology in host-parasite systems. The aim of this thesis was to investigate life-history consequences and parasite transmission dynamics in a terrestrial gastropod infected with parasitic mites, in order to model the epidemiology of the host-parasite system.

The results in **CHAPTER 1** showed that heavily infected *A. arbustorum* are less active and produce fewer eggs than uninfected snails. Furthermore, there was a negative correlation between parasite intensity and winter survival. The reduced winter survival in experimentally infected snails supports the latter finding. In the study we combined observational and experimental approaches. Correlations between parasite infection and fitness components of the host provide only limited information on the causation of the correlation (Zera, 2001). Parasite infection might be the result of the reduced fitness instead of the cause. The experimental data on winter survival, however, show the causality between mite infection and fitness in *A. arbustorum*, and strongly confirm our results from the correlational approach.

A parasite-induced reduction in host reproductive output and survival may affect the dynamics of the host population (Jaenike et al., 1995). However, at the population level, parasites may either stabilize or destabilize their host population (Hudson et al., 2006), and may even lead to local extinction of the host (Deredec and Dourchamps, 2003). A variety of factors influence the outcome of the host-parasite interaction. Besides biological aspects of the host- and parasite species, environmental aspects may shape the dynamics of host- and parasite populations (Koella and Restif, 2001; Wolinska and King, 2009). Thus it is not possible to predict host population dynamics without detailed information on the structure of host- and parasite populations and on the interaction with environmental conditions (Thompson, 1999).

In **CHAPTER 2**, the parasite load of experimentally infected *A. arbustorum* showed high variation among snail families. Phenotypic resemblance among full siblings under

experimental conditions implies that inherited genetic variation may cause this difference (Falconer and Mackay, 1996). The high heritability indicates a strong impact of the host's genetic background on parasite load. However, further aspects including maternal effects may contribute to the parasite resistance of the offspring (Little et al., 2006). Furthermore, we did not consider possible effects of phenotypic variance caused by the dominance variance among full sibs (Falconer and Mackay, 1996).

Adaptive genetic variation is a precondition for parasite-mediated selection on host populations (Carius et al., 2001; Moller et al., 2004). Parasite pressure may favor resistant host genotypes, leading to coevolutionary processes generated by parasite adaptation and by negative frequency-dependent selection on host genotypes (Ladle, 1992). This process is known as Red Queen hypothesis and is one of the mayor hypotheses explaining the maintenance of sex and recombination in animals and plants (Salathe et al., 2008). Coevolution between parasites and their hosts can only occur over long time periods. Since spatial and temporal patterns of *R. limacum* infection in *A. arbustorum* populations are only marginally known, it is difficult to predict coevolutionary processes in *R. limacum* and *A. arbustorum*.

CHAPTER 3 provided experimental evidence that *R. limacum* can be transmitted via soil without physical contact between hosts. Furthermore, *R. limacum* showed a preference to move on fresh snail mucus under experimental conditions. Mucus trails are used by snails to locate mating partners and to discriminate between conspecific and heterospecific individuals (Shaheen et al., 2005). Accordingly, mucus trails may be used by parasites as an interspecific signal in order to locate new hosts and to increase their probability of transmission. However, the meaning of mucus trails in the transmission process of *R. limacum* under natural conditions is unknown. Because of the limited off-host survival of *R. limacum* (Baker, 1970), the importance of mucus trails may be restricted to a rather small spatial scale.

Transmission of *R. limacum* between parasite-infected and parasite-free *A. arbustorum* occurred in pairs with physical contacts, and was slightly affected by parasite intensity of the infected snail. The findings of **CHAPTER 4** suggest that parasite transmission mainly occurs during encounters of snail individuals. Thus, the contact-based transmission

models may be consistent with the transmission biology of *R. limacum*. Host contact networks are a key factor in the transmission of directly transmitted parasites. Increased network connectivity may increase the risk of acquiring an infection (Otterstatter and Thomson, 2007; Godfrey et al., 2009). Contact patterns are highly heterogeneous in social species, violating the assumption of random mixing, on which most mathematical models are based (Perkins et al., 2008). However, the snail *A. arbustorum* is a non-social host. Encounters among adult individuals may most frequently occur during the long-lasting courtship and mating (Baur, 1992). Mating frequency in *A. arbustorum* has been shown to increase with increasing population density (Kupfernagel et al., in press). Transmission may also occur during incidental encounters not related to mating activity, and in snails resting in clumped patterns on single plants (Baur, 1986) and thus infecting juvenile individuals (Baur and Baur, 2005). In contrast to social host species, contact patterns in *A. arbustorum* may be closely related to population density.

The basic reproductive ratio (R_0) is frequently used as a threshold parameter to predict the dynamics of pathogens in host populations. A disease may spread in a susceptible population if $R_0 > 1$ (Heffernan et al., 2005). Basic reproductive ratios obtained in our models revealed a high variation among snail populations and predict a rapid spread of *R. limacum* introduced in susceptible host populations. Considering the effective reproductive ratio (R), in 2 out of 3 *A. arbustorum* populations R was smaller than 1 in model 2, which would predict the extinction of *R. limacum* in the respective populations. This result suggests that R and R_0 might be underestimated in model 2.

Our models predict that the occurrence of *R. limacum* is impeded in host populations with densities below 0.35 – 2.72 snails per m². In fact, a survey of 11 *A. arbustorum* populations revealed that *R. limacum* is not consistently distributed in host populations in Switzerland. *Riccardoella limacum* occurred in 36.4% of the populations examined (Baur and Baur, 2005). Besides host threshold population densities, the distribution of *R. limacum* might be limited by climatic conditions. *Riccardoella limacum* did not occur in alpine *A. arbustorum* populations. The survival of mite eggs in the pulmonary cavity of the host might decrease due to the extended period of snail hibernation at high altitudes (Baur and Baur, 2005).

Basic and effective reproductive ratios were larger in the Nuglar population than in the Weissenstein and Thun population. Such a large R implies higher parasite prevalence than recorded in the Nuglar population. Several mechanisms might explain the relative low parasite prevalence in the high-density population Nuglar. First, the density dependent contact function might level off under high densities as a result of interference competition by mucus trails (Baur, 1988), leading to a reduced transmission in high-density snail populations. In many host-parasite systems transmission functions decrease in response to increasing densities (Fenton et al., 2002). Second, in contrast to our model assumptions, parasite resistance and/or the clearance rate might be higher in the Nuglar population than in the Weissenstein and Thun population. Our assumption that clearance of the infection and resistance to the infection do not occur is based on data from experimentally infected *A. arbustorum* kept under laboratory conditions. Mite infection was successful in 96.5% of the snails infected and clearance of the infection could not be observed (Chapter 2). Third, it is possible that the Nuglar population deviated from the epidemiological equilibrium and parasite prevalence increased in the course of the survey. However, parasite prevalence, which was repeatedly assessed in the Nuglar population, was consistent over time.

OUTLOOK

In the present thesis transmission dynamics of *R. limacum* were modeled for one reproductive season. However, the epidemiology of *R. limacum* may not be constant over time. For instance, among-year variation in environmental conditions may affect the host life-history and consequently shape the host and parasite performance. The implementation of long-term data on parasite-induced life-history responses and host population structure may improve the host-parasite transmission models (Fitze et al., 2004).

Riccardoella limacum did not occur in alpine *A. arbustorum* populations (Baur and Baur, 2005), which suggests that the environmental conditions in the alps impede the spread of *R. limacum*. However, investigation of the influence of climatic conditions on

the development of *R. limacum* is needed to understand the interaction between parasite occurrence and environmental conditions.

In the thesis we considered life-history consequences of *A. arbustorum* infected by an arthropod ectoparasite. However, most host species are infected with a parasite community, consisting of several parasite species (Holmstad et al., 2005). For instance, *Arianta arbustorum* is often infected with parasitic nematodes (Halvorsen and Skorping, 1982). A coinfection with different parasite species may lead to increased within-host competition for host resources, resulting in higher virulence of the parasites involved (VanBaalen and Sabelis, 1995; Alizon and vanBaalen, 2008). Such interactions among parasite species are expected if they exploit the same host resource. Furthermore, ectoparasites often act as vectors for bacterial and viral diseases (Ewald, 1983). With our experimental design we cannot discriminate between ectoparasite-induced and vector-borne effects on life-history of *A. arbustorum*. Experimental infection of host snails should be combined with subsequent clearance of the *R. limacum* infection in order to compare the performance of mite-infected and subsequently parasite-free hosts.

Parasites are known to play a key role in the evolution of sex (Hamilton et al., 1990; Ladle, 1992). The ability to generate genetic variability in offspring by means of recombination is a strong advantage to cope with parasite infection. In return, parasites may shape the allocation of resources in host reproduction. This may lead to an increase in the reproductive effort (Forbes, 1993; Perrin et al., 1996; Gandon et al., 2002) and favor early reproduction in host populations (Hochberg et al., 1992; Restif et al., 2001). Most studies on parasite-induced alteration of host reproduction focused on gonochoristic species, whereas studies investigating the role of parasites in hermaphrodites are scarce. *Arianta arbustorum* and *R. limacum* may serve as a model system to test the impact of parasite infection on resource allocation in simultaneous hermaphrodites. The system may help to understand how hermaphrodites allocate their resources to the male and the female function. Furthermore, the study system may shed light to the patterns of pre- and postcopulatory sexual selection in simultaneous hermaphrodites.

REFERENCES

- Alizon, S. and van Baalen, M. (2008) Multiple infections, immune dynamics, and the evolution of virulence. *Am. Nat.* 172, E150-E168.
- Baker, R.A. (1970) Studies on the life history of *Riccardoella limacum* (Schrank) (Acari, Trombidiformes). *J. Nat. Hist.* 4, 511-519.
- Baur, A. and Baur, B. (2005) Interpopulation variation in the prevalence and intensity of parasitic mite infection in the land snail *Arianta arbustorum*. *Invertebr. Biol.* 124, 194-201.
- Baur, B. (1986) Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). *Holarctic Ecol.* 9, 117-125.
- Baur, B. (1988) Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. *Oecologia* 77, 390-394.
- Baur, B. (1992) Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum* - experiments and an explanation. *Anim. Behav.* 43, 511-518.
- Carius, H.J., Little, T.J. and Ebert, D. (2001) Genetic variation in a host-parasite association: Potential for coevolution and frequency-dependent selection. *Evolution* 55, 1136-1145.
- Deredec, A. and Courchamp, F. (2003) Extinction thresholds in host-parasite dynamics. *Ann. Zool. Fenn.* 40, 115-130.
- Ewald, P.W. (1983) Host-parasite relations, vectors, and the evolution of disease severity. *Ann. Rev. Ecol. Syst.* 14, 465-485.
- Falconer, D.S. and Mackay, T.F.C. (1996) Introduction to quantitative genetics. Longman, Essex.
- Fenton, A., Fairbairn, J.P., Norman, R. and Hudson, P.J. (2002) Parasite transmission: reconciling theory and reality. *J. Anim. Ecol.* 71, 893-905.
- Fitze, P.S., Tschirren, B. and Richner, H. (2004) Life history and fitness consequences of ectoparasites. *J. Anim. Ecol.* 73, 216-226.
- Forbes, M.R.L. (1993) Parasitism and host reproductive effort. *Oikos* 67, 444-450.

- Gandon, S., Agnew, P. and Michalakis, Y. (2002) Coevolution between parasite virulence and host life-history traits. *Am. Nat.* 160, 374-388.
- Godfrey, S.S., Bull, C.M., James, R. and Murray, K. (2009) Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behav. Ecol. Sociobiol.* 63, 1045-1056.
- Halvorsen, O. and Skorping, A. (1982) The influence of temperature on growth and development of the nematode *Elaphostrongylus rangiferi* in the gastropods *Arianta arbustorum* and *Euconulus fulvus*. *Oikos* 38, 285-290.
- Hamilton, W.D., Axelrod, R. and Tanese, R. (1990) Sexual reproduction as an adaptation to resist parasites (a review). *Proc. Natl. Acad. Sci. USA* 87, 3566-3573.
- Heffernan, J.M., Smith, R.J. and Wahl, L.M. (2005) Perspectives on the basic reproductive ratio. *J. R. Soc. Lond. Interface* 2, 281-293.
- Hochberg, M.E., Michalakis, Y. and de Meeus, T. (1992) Parasitism as a constraint on the rate of life-history evolution. *J. Evol. Biol.* 5, 491-504.
- Holmstad, P.R., Hudson, P.J. and Skorping, A. (2005) The influence of a parasite community on the dynamics of a host population: a longitudinal study on willow ptarmigan and their parasites. *Oikos* 111, 377-391.
- Hudson, P.J., Dobson, A.P. and Lafferty, K.D. (2006) Is a healthy ecosystem one that is rich in parasites? *Trends Ecol. Evol.* 21, 381-385.
- Jaenike, J., Benway, H. and Stevens, G. (1995) Parasite-induced mortality in mycophagous *Drosophila*. *Ecology* 76, 383-391.
- Koella, J.C. and Restif, O. (2001) Coevolution of parasite virulence and host life history. *Ecol. Lett.* 4, 207-214.
- Ladle, R.J. (1992) Parasites and sex - catching the Red Queen. *Trends Ecol. Evol.* 7, 405-408.
- Little, T.J., Watt, K. and Ebert, D. (2006) Parasite-host specificity: Experimental studies on the basis of parasite adaptation. *Evolution* 60, 31-38.
- Møller, A.P., Martin-Vivaldi, M. and Soler, J.J. (2004) Parasitism, host immune defense and dispersal. *J. Evol. Biol.* 17, 603-612.

- Otterstatter, M.C. and Thomson, J.D. (2007) Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia* 154, 411-421.
- Perkins, S.E., Ferrari, M.F. and Hudson, P.J. (2008) The effects of social structure and sex-biased transmission on macroparasite infection. *Parasitology* 135, 1561-1569.
- Perrin, N., Christe, P. and Richner, H. (1996) On host life-history response to parasitism. *Oikos* 75, 317-320.
- Restif, O., Hochberg, M.E. and Koella, J.C. (2001) Virulence and age at reproduction: new insights into host-parasite coevolution. *J. Evol. Biol.* 14, 967-979.
- Salathe, M., Kouyos, R.D. and Bonhoeffer, S. (2008) The state of affairs in the kingdom of the Red Queen. *Trends Ecol. Evol.* 23, 439-445.
- Shaheen, N., Patel, K., Patel, P., Moore, M. and Harrington, M.A. (2005) A predatory snail distinguishes between conspecific and heterospecific snails and trails based on chemical cues in slime. *Anim. Behav.* 70, 1067-1077.
- Thompson, J.N. (1999) The evolution of species interactions. *Science* 284, 2116-2118.
- vanBaalen, M. and Sabelis, M.W. (1995) The dynamics of multiple infection and the evolution of virulence. *Am. Nat.* 146, 881-910.
- Wolinska, J. and King, K.C. (2009) Environment can alter selection in host-parasite interactions. *Trends in Parasitology* 25, 236-244.
- Zera, A.J. and Harshman, L.G. (2001) The physiology of life history trade-offs in animals. *Annu. Rev. Ecol. Syst.* 32, 95-126.

PERSONALITIES

Hans Ulrich Schüpbach
Kasernenstrasse 47, 3013 Bern
H.Schuepbach@unibas.ch

Date of Birth: 03.12.1977
Nationality: Swiss
Marital status: Single

EDUCATION

- 2006 – 2009 PhD thesis, Department of Environmental Sciences,
University of Basel
- 2004 – 2005 Diploma thesis, Department of Evolutionary Ecology,
University of Bern
- 2000 – 2003 Biology undergraduate studies, University of Bern
Research practicals in Evolutionary Ecology, Population Genetics and
Conservation Biology
- 1995 - 1999 Elementary teacher diploma,
Höhere Mittelschule Marzili, Bern

RECENT RESEARCH

- 2006 - 2009 Department of Environmental Sciences, University of Basel
PhD Thesis: “Life-history responses, transmission dynamics and
epidemiology in a terrestrial gastropod infected with parasitic mites”
Supervision: Prof. Bruno Baur
- 2004 - 2005 Department of Evolutionary Ecology, University of Bern
Diploma thesis: “Effect of food quality and cannibalism on growth,
development, and population regulation of an ectoparasite”
Supervision: Prof. Heinz Richner

PUBLICATIONS

- Schüpbach H.U. and Baur B. (2008) Parasitic mites influence fitness components of their host, the land snail *Arianta arbustorum*. *Invertebrate Biology* 127: 350–356.
- Schüpbach H.U. and Baur B. (2008) Experimental evidence for a new transmission route in a parasitic mite and its mucus-dependent orientation towards the host snail. *Parasitology* 135: 1679–1684.
- Schüpbach H.U. and Baur B. (2010) Contact-based transmission models in terrestrial gastropod populations infected with parasitic mites. *International Journal for Parasitology*, in press.
- Schüpbach H.U. and Baur B. (2010) Within- and among-family variation in parasite load and parasite-induced mortality in the land snail *Arianta arbustorum*, a host of parasitic mites. *Journal of Parasitology*, in press.

CONFERENCE CONTRIBUTIONS

- Schüpbach H.U. and Baur B. (2008) Parasitic mites influence fitness components of their host, the land snail *Arianta arbustorum*. Biology 08, Lausanne, Switzerland.
- Schüpbach H.U. and Baur B. (2008) Parasitic mites and sexual selection in a simultaneous hermaphrodite, the land snail *Arianta arbustorum*. ASAP meeting, Neuhausen, Germany
- Schüpbach H.U. and Baur B. (2007) Effects of parasitic mites on behavior and life-history traits of their host, the land snail *Arianta arbustorum*. World congress of Malacology, Antwerp, Belgium

COURSES AND WORK EXPERIENCE

- | | |
|-------------------|---|
| 2006 – 2009 | Courses at the PhD Programme; Zurich-Basel Plant Science Center. |
| October 2008 | ASAP-workshop: Sexual strategies in plants and animals. Neuhausen, Germany. |
| September 2007 | The Natural History of Host-Parasite Interactions. London, England. |
| August 2006 | Workshop 3 rd Hermaphrodite-Meeting, Tübingen, Germany. |
| May 2006 | Workshop Evolutionary Biology, Guarda, Switzerland. |
| May – August 2005 | Assistant in research and teaching, Zoological Institute, University of Bern. |

DURING MY STUDIES I ATTENDED LECTURES BY;

University of Bern

J.P. Airoidi, B. Ammann, C. Ammann, M. Aragno, R. Arlettaz, H. Balsiger, U. Baumann, R. Brändle, B. Erni, O. Eugster, L. Excoffier, D. Felix, U. Feller, T. Frank, H.J. Geiger, M. Güntert, R. Häner, H. Imboden, T.W. Jungi, A. Kirchhofer, J. Kohli, C. Kropf, C. Kuhlemeier, B. Lanzrein, C. Largiader, S. Leutwyler, C. Meier, C. Müller, P. Munz, W. Nentwig, D. Rentsch, H. Richner, H. Riedwyl, I. Roditi, C. Rothen, P. Schelling, P. Schmid, D. Schümperli, M.E. Schweingruber, T. Seebeck, B. Stadler, T. Stocker, M. Taborsky, A. Valsangiacomo, J. Zettel

University of Basel

B. Baur, D. Ebert, A. Erhardt, T. Fabbro, P. Nagel, P. Stoll