

Raine Kortet

Parasitism, reproduction and sexual  
selection of roach, *Rutilus rutilus* L.

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella  
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa (YAA303)  
tammikuun 18. päivänä 2003 kello 12.

Academic dissertation to be publicly discussed, by permission of  
the Faculty of Mathematics and Science of the University of Jyväskylä,  
in the Building Ambiotica, Auditorium YAA303, on January 18, 2003 at 12 o'clock noon.



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2003

Parasitism, reproduction and sexual  
selection of roach, *Rutilus rutilus* L.

Raine Kortet

Parasitism, reproduction and sexual  
selection of roach, *Rutilus rutilus* L.



UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2003

Editors

Jukka Särkkä

Department of Biological and Environmental Science, University of Jyväskylä

Pekka Olsbo, Marja-Leena Tynkkynen

Publishing Unit, University Library of Jyväskylä

URN:ISBN 9513913562

ISBN 951-39-1356-2 (PDF)

ISBN 951-39-1396-1 (nid.)

ISSN 1456-9701

Copyright © 2003, by University of Jyväskylä

## ABSTRACT

Kortet, Raine

Parasitism, reproduction and sexual selection of roach, *Rutilus rutilus* L.

Jyväskylä: University of Jyväskylä, 2003, 37 p.

(Jyväskylä Studies in Biological and Environmental Science,

ISSN 1456-9701; 118)

ISBN 951-39-1356-2

Yhteenveto: Loisten ja taudinaiheuttajien rooli kalan lisääntymisessä ja seksuaalivalinnassa

Diss.

One of the main issues in immunological ecology is the role of immune defence in the evolution of life-history traits, i.e. the investment in reproduction at the cost of immune function. Moreover, theories of parasite-mediated sexual selection suggest that secondary sexual characters are connected to parasitism. For this thesis, I studied aspects of fish reproduction and sexual selection with respect to defence against parasites and pathogens. As a model species I used roach, *Rutilus rutilus*. In the seasonal cycle of fish immune defence, the relative size of the spleen and the chemotactic migration activity of head kidney granulocytes decreased immediately before and after spawning, respectively. However, breeding-related changes in other measurements (phagocytosis activity of head kidney granulocytes, blood IgM concentration, white cell count and red cell count) were absent or inconsistent. This suggests that the different parts of the immune system may have different temporal patterns. Moreover, epidermal papilloma disease outbreak peaked around the spawning period in both sexes. Males and large fish had a higher prevalence of papilloma tumours. The gender dependence in the disease prevalence found in this study may indicate differences in stress and immunocompetence between male and female roach. Sexual ornamentation of male roach, the breeding tubercles, signalled a long-term resistance of males against the locally most abundant parasite in the study, *Rhipidocotyle campanula*. Moreover, breeding tubercle ornamentation was associated with dominance status in intrasexual prespawning interactions. In addition, raised circulating androgen levels were related to high breeding tubercle ornamentation, but interestingly, also to increased prevalence of papilloma disease. Thus, I propose that, in the present system, the character that a male roach signals by his sexual ornamentation may be resistance against parasites (*R. campanula*), and that papillomatosis occurring during spawning is an element which contributes to the honesty of the signal. The results in the thesis support the hypothesis of a trade-off between reproduction and immune defence and the hypothesis of parasite-mediated sexual selection. Thus, parasites and pathogens may have an appreciable impact on the evolution of life histories and sexual selection of fish.

Key words: Breeding; Hamilton and Zuk hypothesis; immunocompetence handicap hypothesis; immunoecology; life-history theory; parasites; *Rutilus rutilus*; sexual selection; trade-offs.

*R. Kortet, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40014 University of Jyväskylä, Finland*

**Author's address** MSc Raine Kortet  
Department of Biological and Environmental Science  
University of Jyväskylä  
P.O. Box 35  
FIN-40014 University of Jyväskylä, Finland  
E-mail: rkortet@cc.jyu.fi

**Supervisors** Dr., Docent Jouni Taskinen  
Department of Biological and Environmental Science  
University of Jyväskylä  
P.O. Box 35  
FIN-40014 University of Jyväskylä, Finland  
E-mail: jtaskine@cc.jyu.fi

Dr., Docent Ilmari Jokinen  
Department of Biological and Environmental Science  
University of Jyväskylä  
P.O. Box 35  
FIN-40014 University of Jyväskylä, Finland  
E-mail: ejokine@cc.jyu.fi

**Reviewers** Dr. Claus Wedekind  
Institute of Cell, Animal and Population Biology  
University of Edinburgh  
West Mains Road  
Edinburgh EH9 3JT Scotland, UK  
E-mail: c.wedekind@ed.ac.uk

Dr., Docent Jukka Jokela  
Department of Biology  
University of Oulu  
P.O. Box 3000,  
FIN-90014, Oulu, Finland  
E-mail: jwjokela@cc.oulu.fi

**Opponent** Dr. Michael Siva-Jothy  
Dept. of Animal & Plant Sciences  
University of Sheffield  
Sheffield S10 2TN, UK  
E-mail: M.Siva-Jothy@sheffield.ac.uk

## CONTENTS

List of original publications .....	6
Responsibilities of Raine Kortet in the articles of this thesis .....	7
1 INTRODUCTION .....	9
1.1 Life-history trade-off and immune defence .....	9
1.2 Parasite-mediated sexual selection .....	10
2 ROLE OF PARASITES AND PATHOGENS IN REPRODUCTION AND SEXUAL SELECTION; RESULTS AND DISCUSSION .....	14
2.1 Reproductive biology of roach ( <i>Rutilus rutilus</i> ) .....	14
2.2 Breeding-related seasonal changes in condition, health state and immune defence .....	15
2.3 Epidermic papillomatosis .....	16
2.4 Breeding tubercles .....	18
2.5 Breeding tubercles, immune defence and parasites .....	19
2.6 Androgens, papillomatosis and breeding tubercles .....	20
2.7 Breeding tubercles, dominance behaviour and papillomatosis .....	22
3 CONCLUSIONS .....	25
<i>Acknowledgements</i> .....	27
YHTEENVETO (Résumé in Finnish) .....	28
REFERENCES .....	30

## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original papers, which will be referred to in the text by their Roman numerals (I-V).

- I Kortet, R., Taskinen, J., Sinisalo, T. & Jokinen, I. 2002: Breeding-related seasonal changes in immunocompetence, health state and condition of the cyprinid fish, *Rutilus rutilus*, L. ***Biological Journal of the Linnean Society***, in press.
- II Kortet, R., Taskinen, J. & Vainikka, A. 2002: Epizootic cutaneous papillomatosis in roach *Rutilus rutilus*: sex and size dependence, seasonal occurrence and between population differences. ***Diseases of Aquatic Organisms***, 52(3): 185-190.
- III Taskinen, J. & Kortet, R. 2002: Dead and alive parasites: sexual ornaments signal resistance in the male fish, *Rutilus rutilus*. ***Evolutionary Ecology Research***, 4: 919-929.
- IV Kortet, R., Vainikka, A., Rantala, M., Jokinen, I. & Taskinen, J. 2002: Sexual ornamentation, androgens and papillomatosis in roach (*Rutilus rutilus*). ***Evolutionary Ecology Research***, in press.
- V Kortet, R., Taskinen, J., Vainikka, A. & Ylönen, H. 2002: Breeding tubercles, papillomatosis and dominance behavior of male roach (*Rutilus rutilus*) during the breeding period. **Submitted manuscript.**



## **Responsibilities of Raine Kortet in the articles of this thesis**

Paper I. The study was jointly planned by all the authors and the data were mainly collected by Raine Kortet, Jouni Taskinen and Tuula Sinisalo. I was responsible for writing the article.

Paper II. I planned the study together with Jouni Taskinen. I collected the data with him and Anssi Vainikka. I wrote the paper.

Paper III. The study was mainly planned by Jouni Taskinen. We collected the data and wrote the article together.

Paper IV. I planned the study and performed it with Anssi Vainikka. Other co-authors contributed to data analysis and manuscript writing, but I was main responsible for writing the article.

Paper V. I was responsible for planning the study. The experiments were mainly done with Anssi Vainikka. Other co-authors contributed to data analysis and manuscript writing. However, I was main responsible for writing the article.

Jyväskylä October 20th, 2002

Raine Kortet

# 1 INTRODUCTION

## 1.1 Life-history trade-offs and immune defence

Since an organism can be seen as a way for genes to move to the next generation, it might seem, at first, logical to assume that an optimal organism should live as long as possible and reproduce all the time by maximizing all its fitness-related traits. However, in addition to its genetic constraints, an organism is bound by phenotypical constraints as well as by constraints of available energy and nutrients. Effort in one aspect of reproduction detracts from other aspects. According to life-history theory, organisms are expected to have trade-offs between different life-history traits, such as age at maturity, generation time, and number, size, and sex ratio of offspring (Roff 1992, Stearns 1992). Recent results also indicate a trade-off between life-history traits and immune defence (reviewed by e.g. Lochmiller & Deerenberg 2000, Norris & Evans 2000). Thus, immunological defence has attracted increasing interest in ecology and evolutionary biology. One of the main issues in immunological ecology is the role of immune defence in the evolution of life-history traits, i.e. the investment in reproduction at the cost of immune function (Sheldon & Verhulst 1996).

The host immune system fights against parasites and diseases to reduce the fitness cost of parasitism. In studies of parasite-mediated sexual selection, host immune functions have been investigated at the time of mating in relation to the expression of secondary sexual characters (e.g. Folstad & Karter 1992, Hillgarth & Wingfield 1997). However, immunological parameters may be subject to rapid temporal changes at the time of breeding due to possible resource limitations (trade-off between immune system and reproduction), or either adaptive or nonadaptive immunomodulative action of sex hormones (Hillgarth & Wingfield 1997). Indeed, according to the immunocompetence handicap and resource reallocation hypotheses of sexual selection (Folstad & Karter 1992, Wedekind & Folstad 1994) testosterone reduces immune defence of males during breeding. The breeding period may also cause physiological

stress, which can *per se* affect immune functions (reviewed by Buchanan 2000). In birds, experimental manipulations of brood size and reproductive effort have yielded empirical evidence for the immunological cost of reproduction (e.g. Sheldon & Verhulst 1996, Deerenberg et al. 1997, Nordling et al. 1998, Ilmonen et al. 2000).

The vertebrate immune system is under hormonal control (e.g. sex hormones and corticosteroids) and is affected by seasonal environmental changes via the neuroendocrine system (Zapata et al. 1992). In fishes, for example, sex hormone levels undergo remarkable changes during breeding (e.g. Rinchard et al. 1997, Kime 1998, Kestemont et al. 1999) which may affect the immune system in various ways (Slater & Schreck 1993, Slater & Schreck 1998, Watanuki et al. 2002). Several studies have demonstrated that organisms show great flexibility in their physiology (Piersma & Lindström 1997), and measures of immune response, such as size of lymphoid organs, are often dependent on condition (Møller et al. 1998). Thus, studying breeding-related physiological responses to seasonal variation may contribute to our understanding of how different patterns of life-history traits have evolved.

Seasonal changes in immunocompetence are predicted by the hypothesised trade-off between reproduction and self-maintenance, whereby immune function is a measure of self-maintenance and reproductive effort is seasonally dependent. In general, seasonal changes in the immune system are found in a wide range of animal species (see reviews in Zapata & Cooper 1990, Nelson & Demas 1996). The existence of temporal changes in immunocompetence associated with breeding is widely accepted, yet poorly studied, especially in wild populations. Earlier studies in captive fishes indicate dysfunction in immune defence during the reproductive period (Iida et al. 1989, Slater & Schreck 1998, Hou et al. 1999).

In the first part of my thesis (papers I and II), I studied the role of immune defence in life-history trade-offs. I examined in two populations how the seasonality of different aspects of fish immune defence, health state and condition is connected to the reproduction period (I). I also studied the spawning-related temporal patterns of epidermic papilloma disease and its dependence on gender (II). Detailed descriptions of the materials and methods of the studies are given in the original papers.

## 1.2 Parasite-mediated sexual selection

Darwin (1871) introduced sexual selection as separate from natural selection. Sexual selection arises when certain individuals have higher mating success compared to others. It may occur due to choosy partners of the opposite sex or as a result of intrasexual competition. Sexual selection is suggested to be strongest in the sex with higher potential reproductive rate and lower investment in parental care, which is in the most species the male (Clutton-

Brock & Vincent 1991; Andersson & Iwasa 1996). Moreover, females have been shown to prefer males with elaborated secondary sexual characters and the mating skew is notably high in lek-like mating systems (Andersson 1994; Höglund & Alatalo 1995).

Several theories have been proposed to explain the evolution of extravagant secondary sexual ornaments. Traditionally, these theories have been divided to the 'Fisherian models' and the 'good genes' hypotheses. The Fisherian self-reinforcing theory (Fisher 1930) suggests that both the male trait and female preference will be genetically coupled creating a situation often referred to as "runaway selection". Traits that were initially attractive because they revealed the bearer's ability to adapt to their environment remain attractive only because they are attractive to females (Pomiankowski & Iwasa 1998). This is unlike the 'good genes' hypotheses proposed subsequently. Zahavi's handicap hypothesis (1975, 1977) suggests females prefer elaborately ornamented males, because the handicapping (i.e. disadvantageous to male survival) ornaments function as honest signals to females of male quality. A good quality male will survive and succeed in its environment in spite of the handicap associated with his ornaments. However, currently the dichotomy between Fisherian runaway process and 'good genes' hypothesis is faded off, since they have been modelled to work as different ends of the same sexual selection continuum (Kokko et al. 2002). In the recent meta-analysis conducted by Møller & Alatalo (1999), 'good genes' based sexual selection was found to work widely across taxa, but the effect was relatively minor. Moreover, there was a reducing effect of publication year on the viability-based sexual selection indicating publication biases during the paradigm shifts of this debated issue. Interestingly, in whitefish, potential mate selection in respect to sexual ornaments has lately been observed to give notable genetic benefits measured as offspring viability (Wedekind et al. 2001). Likewise, in sticklebacks, offspring of brightly ornamented males have been found to be more resistant to parasites than offspring of dullly coloured males (Barber et al. 2001).

Hamilton & Zuk (1982) proposed that secondary sexual characters could specifically signal genetically based parasite resistance, and may have evolved via mate choice. Thus, by choosing an elaborately ornamented male a female may acquire for her offspring genes needed for resistance for the predominant parasites at that time. Since that seminal paper, the role of parasites and immunological defense in host sexual selection has been a subject of growing interest. The original hypothesis by Hamilton & Zuk (1982) (HZH) has been tested by examining male ornamentation in relation to parasite resistance by using parasite load or immune function as a measure of parasite resistance. Comparative studies on parasite loads in relation to ornamentation have yielded mixed evidence for and against the hypothesis as reviewed by e.g. Hamilton & Poulin (1997) and Møller et al. (1999). In general, studies based on measures of immune function have provided stronger evidence for the hypothesis than those based on measures of parasite load (Møller et al. 1999). However, so far a male's ability to directly eliminate its natural parasites has not been used as a measure of resistance. This approach would be crucial, since

the original hypothesis suggests coevolutionary cycles between the host and parasite as an underlying force in the evolution of sexual selection (Hamilton & Zuk 1982). Coevolutionary cycles, on the other hand, are most probable among local hosts and parasite populations specialized to their hosts (Ebert 1994, Lively 1999).

Folstad & Karter (1992) presented a mechanistic extension to the HZH, - the immunocompetence handicap hypothesis (ICHH) - which predicts that the elevated levels of immunosuppressive androgens (or other self-regulating biochemicals that increase the expression of secondary sexual characters, but simultaneously reduces the immunity) are unavoidably needed to produce and maintain effective sexual ornaments. According to the ICHH, male sexual ornamentation should be an honest indicator to females of male quality, since only a genetically high quality male can afford and tolerate costs of decreased defence against parasites and pathogens. In the HZH, the emphasis is in the coadapational cycles between host and parasite as an underlying force to maintaining variation in the traits, while in the ICHH, the emphasis is more in regulating mechanisms between sexual ornamentation, hormones and quantity of the immune defence (see also Westneat & Birkhead 1998).

Following the proposition of the ICHH, several empirical studies have been conducted concerning the issue and the number of these studies is increasing. Recent results have been both supportive (e.g. Skarstein & Folstad 1996, Saino et al. 1997, Kurtz & Sauer 1999, Verhulst et al. 1999, Evans et al. 2000, Peters 2000, Poiani et al. 2000, Barber et al. 2001, Rantala et al. 2002, Rantala & Kortet 2002), contrary (Hillgarth & Wingfield 1997, Hasselquist et al. 1999), or ambiguous (Liljedal et al. 1999) to different aspects of the ICHH. Moreover, some modifications and extensions to the ICHH have been suggested, e.g. the immune redistribution hypothesis (Braude et al. 1999), resource allocation hypothesis (Wedekind & Folstad 1994), sperm protection hypothesis (Folstad & Skarstein 1997, Hillgarth et al. 1997) and the hypothesis concerning different routes between genes, condition, resistance, immunopathology and advertising (Westneat & Birkhead 1998). However, the original ICHH is criticised by Wedekind & Folstad (1994) and by Penn & Potts (1998) due to hypothesised maladaptivity of immunosuppressive action of androgens (but see argue against criticism in Hillgarth & Wingfield 1997). Personally, I think that androgen-mediated immunosuppression is, at least in some extent, an adaptive resource reallocation process that is limited by condition, i.e. energy reserves. Immunosuppression may also partly occur due to adaptive avoidance of autoimmune reactions during an intensive mating period (Råberg et al. 1998, Westneat & Birkhead 1998). Also in that scenario female may get reliable information of male's quality by evaluating his sexual ornamentation. Anyway, more studies with different species are needed to verify the predictions of the immunocompetence-related hypotheses of sexual selection. Most of the studies conducted so far have used birds and have concentrated on metazoan parasites, but not to bacterial and viral diseases. To my knowledge, there are no previous studies of the hormonal predictions of the ICHH in fishes.

In addition to quality-indicating signals for females, ornaments of sexual selection have also been found to work as weapons or badges of status in intrasexual contests (Berglund et al. 1996). Male-male competition may be an important factor determining reproductive success in lek-like breeding systems (Andersson 1994, Höglund & Alatalo 1995). When a male is not likely to be chosen by females, he would benefit by investing more energy in production of status badges or weapons to aid successful male-male competition (Müller & Ward 1995). Since the effect of parasitism has been suggested to be important in intersexual selection, parasitism may play a role also in intrasexual selection (however, see Hamilton & Poulin 1995, Barber 2002).

In the second part of my thesis (papers III, IV and V), I studied the predictions of the HZH and ICHH and the roles of the sexual ornamentation and the papilloma skin disease in male-male prespawning interactions. In studies III and IV, I monitored the relationships between sexual ornamentation (i.e. breeding tubercles), parasite load and parasite resistance, androgens and spawning papillomatosis. The fifth study was a set of behavioural trials, in which I explored how the breeding tubercles and papillomatosis were related to male dominance status in intrasexual prespawning interactions. Detailed descriptions of the materials and methods of the studies are reported in the original papers (III-V).

## **2 ROLE OF PARASITES AND PATHOGENS IN REPRODUCTION AND SEXUAL SELECTION; RESULTS AND DISCUSSION**

### **2.1 Reproductive biology of the roach (*Rutilus rutilus*)**

Roach (*Rutilus rutilus* L.) is a cyprinid fish spawning in spring in large groups in relatively shallow waters. Individuals often migrate to the spawning sites (Kestemont et al. 1999, L'Abée-Lund & Vøllestad 1985, Mills 1991) such as littoral area, bays, creeks and small ponds in which water warms early in the spring. Roach use an external, phyto-lithophil spawning strategy and breeding sites can vary considerably between populations and locations (Mills 1981, Diamond 1985, Mills 1991, Gillet & Dubois 1995).

Roach breeds using an intensive and short-term mating system. Female roach have strong individual preferences and spawning is not random (Wedekind 1996). Females are often bigger than males (Spivak et al. 1979, Diamond 1985, Vøllestad & L'Abée-Lund 1987). Roach show no parental care, and the mating is non-resource based lek-mating as defined by Höglund & Alatalo (1995): females obtain only genes from the males, and males can not monopolise resources to gain matings. Moreover, the costs for females of searching male groups may be low. In some studies, females have been found to choose males having a territory, and multi-male fertilization is common (Diamond 1985, Wedekind 1996). However, there is no clear association between the male chosen and the site of oviposition in roach (Wedekind 1996). Spawning males can have bourgeois and/or parasitic roles (Wedekind 1996). Moreover, spawning behaviour of roach is not as clearly territorial as the spawning of another cyprinid species, the bream (*Abramis brama* L.) (Svärdson 1951, Mills 1991, Poncin et al. 1996).

Male roach produce sexual ornamentation (breeding tubercles); tubercles are suggested to give to female detailed information about a male's parasite

load (Wedekind 1992). In studies III, IV, V I examined the breeding tubercles of roach in the context of sexual selection.

There is a high frequency of simultaneous parasitic spawning actions in roach (Svårdson 1951; Diamond 1985; Wedekind 1996), which may indicate that sperm competition might be an important intrasexual selective force (Taborsky 1998). However, in roach, parasitic spawning is not a specific alternative tactic of the male but rather an opportunistic behaviour, since the territory owners and sneakers do not differ clearly by their morphology, except sometimes in size, unlike e.g. jacks and hooknoses among salmonids as described by Wootton (1990).

As an iteroparous species, roach has to balance its reproductive effort between present and future reproduction, which may lead to fixed physiological trade-offs in its life-history traits (Roff 1992, Stearns 1992).

## **2.2 Breeding-related seasonal changes in condition, health state and immune defence**

Life-history theory predicts a trade-off between reproduction and immune defence (Sheldon & Verhulst 1996). Therefore, in the seasonal pattern of immunocompetence, there should be a decrease during the breeding period in species with an active and intensive mating. Since spawning of roach is physically demanding, I predicted clear breeding related-changes in condition, health state and immunocompetence. I observed some indication of breeding-related increase in haematocrit and decrease in relative body weight in study I, which suggests that the breeding period of roach is physically demanding and stressful (Munkittrick & Leatherland 1982, Wester et al. 1994, Bolger & Connolly 1989).

In study I, the relative size of the spleen decreased in both populations and in both sexes during breeding. Spleen is assumed to be an essential secondary lymphatic organ in fishes (Manning 1994). Decreased size of the spleen in the spawning period and quick recovery after breeding may attest to the existence of fast physiological trade-offs (see Piersma & Lindström 1997). Spleen size is also known to decrease during the breeding season in captive fishes (Zapata et al. 1992) and birds (Nelson & Demas 1996). Furthermore, in both populations, the chemotactic migration activity of head kidney granulocytes decreased during mating. The head kidney is presumed to play an important role as a lymphatic organ in fishes (Manning 1994). Granulocytes are a part of the non-specific defence in fish (Secombes 1996). The migration activity of roach granulocytes has been shown to decrease under stress, e.g. under UV-exposure (Salo et al. 1998).

Unlike in the cases of spleen size and head kidney granulocyte activity, the breeding-related seasonal changes in the numbers of white blood cells, blood immunoglobulin concentration and granulocyte phagocytosis activity



were equivocal. The number of white blood cells reflects the general state of health and immune response in fish (Wester et al. 1994). An increased number of leukocytes, especially granulocytes, is a common consequence of infection (e.g. Ellis 1986). Phagocytosis activity (respiratory burst) of head kidney granulocytes manifests the function of those cells when challenged. Therefore, the results of this study suggest that, while some parts of roach immune system may be suppressed during mating, other parts may remain unaffected. The present results indicate a breeding-related impairment at least in some parts of the immune defence system of roach. Thus the results are partly in accordance with the hypothesised trade-off between reproduction and immunocompetence.

One of the main results of study I was that I found a remarkable variation between seasonal patterns of different immunocompetence measures. I also found seasonal patterns of immune characteristics to differ between populations and sexes. This may indicate a variation in response of the fish immune system to temporal and spatial environmental changes (including pathogens and parasites). Fluctuating seasonality in immunocompetence can give rise to a problem in studies including a parasite's role in sexual selection, if there are interactions between the temporal pattern of different immune functions and the expression of sexual ornaments and if the immune measures are studied only during breeding period. Indeed, such an interaction was found in jungle fowl by Zuk & Johnsen (1998), where differently ornamented males had disparities in their seasonal immunity patterns. In addition, my results support the view that the use of any single aspect of immunity as a general unitary measure of immunocompetence is not to be recommended (Lochmiller 1995, Siva-Jothy 1995, Zuk & Johnsen 1998).

### **2.3 Epidermic papillomatosis**

Epidermal papillomatosis is a virus-induced disease, which has been described from several fish species (e.g. Bylund et al. 1980, Möller & Anders 1986, Lee & Whitfield 1992, Møllergaard & Nielsen 1995, Premdas et al. 1995). However, the viral agents of papillomata have not been visualised or defined in all studies. Papillomata may erupt in fish due to various physiological stress factors, such as anoxia or environmental pollutants (Møllergaard & Nielsen 1995, Premdas et al. 1995). The clinical symptoms of papillomatosis include white, smooth, loosely attached ovoid tumours on the skin and fins of fish. During severe infection, fish skin may be totally covered by hyperplastic epidermis. The persistent latent infectious agents of papilloma are suggested to be present in the population all the time, and only part of population may get the disease with tumours (Lee & Whitfield 1992). In smelt, large fish have been reported to have the highest papilloma tumour prevalences and intensities (Møller & Anders 1986, Lee & Whitfield 1992). Prior to my study, several observations of

epidermal skin diseases were made in roach in the present study areas, but detailed descriptions of papillomatosis on roach were lacking.

In study II, epidermal papillomatosis was found to occur in the majority of the lakes studied during the spawning periods in 1999 and 2000. Thus, the papillomatosis seems to be a common disease of roach in Finland. Seasonality in the occurrence of disease showed a peak around the spawning period. I also observed a male-biased gender dependence in the presence of papillomatosis, and that pattern was similar in most of the populations where the tumours were present. The length of the fish was also related positively to occurrence of papillomatosis in six of the eight populations.

Sexual maturity and reproduction cause hormonal and physiological stress (see e.g. Pottinger & Carrick 2000), which may induce papillomatosis outbreak during the spawning period. Several indications of dysfunction in fish immune defence during reproduction are known (Iida et al. 1989, Slater & Schreck 1998, Hou et al. 1999). Moreover, in study I, breeding-related seasonal reductions in some aspects of immunity were found. A decrease in the fish immunocompetence may increase the risk of infections and diseases during sexual maturation and reproduction. Therefore, the reason for the papillomatosis outbreaks during spawning may be the lowered immunological condition of fish at that time due to physical stress and hormonal changes. In support of this argument, the prevalence and abundance of gyrodactylid monogenean parasites also peaks in the spring during the spawning period of roach (Koskivaara et al. 1991). Epidermic spawning papillomatosis has also been described in smelt (Möller & Anders 1986, Lee & Whitfield 1992). Papilloma virus may be present in the fish stock all the time, but the spawning stress and changing sex hormone levels may stimulate its manifestation, as has been suggested by Lee & Whitfield (1992). At least some fish may recover from the disease, since I found some roach specimens with presumably healed tumours, but the latent infection may remain.

The observed male-biased gender dependence of papillomatosis may be explained by the development of the breeding tubercles. Clear morphological changes in skin, like breeding tubercles, may *per se* increase the risk of epidermal diseases in males, because growing or transient body tissue may be more vulnerable to tumour-inducing infections. This could contribute to the observed higher prevalence of papillomatosis in male fish. On the other hand, sex hormones are commonly associated with decreased immunocompetence (Iida et al. 1989, Slater & Schreck 1998, Hou et al. 1999), and androgens may have an effect on papilloma disease outbreaks. In salmon, Bylund et al. (1980) suggested an association of papillomatosis with physiological, basically hormonal changes. In fact, Premdas et al. (2001) found that testosterone itself enhanced the development of papillomata in white sucker *Catostomus commersoni* Lacepède. Moreover, my results in study IV also indicated papillomatosis to be connected with testosterone levels. The observed gender dependence in the disease prevalence may also indicate that the possible trade-off between reproduction and immune defence may be more clear in males than among females. Roach spawning is an intensive lek-like mating (Wedekind 1996),

which may be more stressful for males than females and thus induce more papillomatosis among males. The potential role of epidermal injury in aggressive or sexual encounters of males may also be important in papilloma tumorigenesis, since replicating cells in the epidermis might be the main substrate for neoplasms (Walter & Israel 1987).

In addition to gender dependence, I found that length affects the occurrence of papilloma disease. Similar size dependence as I observed, has also been found in earlier studies with smelt (Möller & Anders 1985, Lee & Whitfield 1992). This phenomenon might also be explained by hormone-related changes in immune defence, if larger fish have higher levels of immunomodulative androgens (e.g. Cheek et al. 2000). Alternatively, the larger (i.e. older) fish have a higher probability of having been exposed to presumably chronic papillomavirus. This result is also in line with 'terminal investment' of life history theory, if spawning papillomatosis is a consequence of reproductive effort in general. In fishes, reproductive effort is observed to increase with age (Roff 1992).

Spawning papillomatosis may have an impact on roach populations since the fishes with severe infections may have an increased risk of secondary fungal or bacterial infections, or of predation. The papillomatosis may also increase mortality of fishes *per se* (Sano et al. 1991).

## 2.4 Breeding tubercles

Breeding tubercles are keratin-based epidermal nodules, which are common in many fishes, mainly in males. The breeding tubercles of teleosts are induced by several pituitary and sex hormones and they fall off shortly after spawning (see review by Wiley & Collette 1970). The development of breeding tubercles may take weeks rather than days (Wiley & Collette, 1970). The role and evolution of breeding tubercles are not well known. Breeding tubercles may be used for conspecific recognition (Vladykov et al. 1985), or for protection against mechanical injuries (Ahnelt & Keckeis 1994). Müller & Ward (1995) suggested that breeding tubercles may be used as weapons in intense pre-spawning behaviour of males (defence of nests and territories). However, Wiley & Collette (1970) proposed that tubercles originally evolved to allow breeding individuals to maintain close contact during the spawning as a means to ensure fertilization of the eggs. Breeding tubercles may also act as hydrodynamic or tactile stimulators of females during courtship. However, to my knowledge, no previous behavioural studies have been conducted to examine the role of breeding tubercles as a sexual ornament.

Recently, in whitefish, the breeding tubercle ornamentation has found to indicate offspring survival (Wedekind et al. 2001). In roach, the breeding tubercles are thought to give females detailed information about a male's parasite load (Wedekind 1992) and to act as a sexual ornament indicating a

male's quality. According to my observations, there is a remarkable variation on the breeding tubercles between and within wild roach populations.

## 2.5 Breeding tubercles, immune defence and parasites

Hamilton & Zuk (1982) proposed that secondary sexual characters could signal genetically based parasite resistance. In study III, I examined ornamentation of male roach from five populations in relation to (a) host long-term resistance (proportion of dead parasites; two parasite species), (b) parasite load (intensity/prevalence; five parasite species), (c) immune function (spleen size) and (d) somatic condition.

I found the proportion of dead *Rhipidocotyle campanula* Dujardin (Digenea, Bucephalidae) to correlate positively with male sexual ornamentation in all three of the populations (Konnevesi, Jyväsjärvi, Saravesi) where the parasite was abundant (III). The result suggests that ornamentation may signal parasite resistance in roach, which is in accordance with the prediction of the HZH (Hamilton & Zuk 1982). Moreover, I did not find evidence that ornamentation correlates with immune function, condition, parasite load or resistance against other, less prevalent parasites.

*R. campanula* was the parasite that was locally most prevalent (100% infection) and abundant (on average 14, 9 and 88 parasite specimens per host in Lakes Konnevesi, Jyväsjärvi and Saravesi, respectively) in the study populations. Bucephalid digeneans, like *R. campanula*, have also been found to be virulent to their fish hosts (e.g. Hoffmann et al. 1990). If ornaments signal specific resistance against *R. campanula*, this would be in line with the idea that host-parasite coevolutionary cycles could drive the evolution of sexual selection (Hamilton & Zuk 1982). All else being equal, host-parasite coevolutionary cycles can be expected to be most probable to the locally most abundant parasites (Ebert 1994, Lively 1999).

Wild roach has been shown to produce specific antibodies against *Rhipidocotyle fennica* Gibson, Taskinen & Valtonen, a close relative of *R. campanula* (Aaltonen et al. 1997). Therefore a specific humoral immune response, and specific resistance, against *R. campanula* is possible. However, it can not be ruled out that ornaments signal general parasite resistance. On the other hand, it is possible that ornaments do not signal parasite resistance as such, but reflect good condition. However, this seems improbable since the present results indicated no relationship between ornamentation and fish condition.

## 2.6 Androgens, papillomatosis and breeding tubercles

Since papilloma tumours may somehow be linked to testosterone levels (Premdas et al. 2001), this disease may provide a good tool to model ICHH of sexual selection (Folstad & Karter 1992), if the costs of papilloma virus differ between variously ornamented males. One of the predictions of that hypothesis is that sexual ornaments, i.e. breeding tubercles in the case of roach, are produced by immunomodulative sex hormones. In study IV, I examined circulating testosterone and 11-ketotestosterone levels, sexual ornamentation and epidermal papillomatosis, of male roach during the breeding period.

The results in study IV are consistent with the ICHH; there was a positive relationship between fish androgen levels, sexual ornamentation and papilloma skin disease. Male roach, which had elevated expression of sexual ornamentation, had high levels of testosterone and 11-ketotestosterone as well as higher papillomatosis prevalence. Likewise, Skarstein & Folstad (1996) found that sexual ornamentation of male Arctic charr, *Salvelinus alpinus* L. was positively related to intensities of parasites, and in addition, negatively related to lymphocyte count.

The relationship between the expression of secondary sexual characters and testosterone is widespread among a variety of species, and testosterone is considered in most cases to be the main sex steroid needed in the production of sexual ornamentation (Hillgarth & Wingfield 1997, Verhulst et al. 1999, Evans 2000). In teleost fishes, 11-ketotestosterone is suggested to act as the main androgen, but testosterone is also important (Borg 1994). High levels of 11-ketotestosterone have been found associated with the development of the head crest, the badge of status in the spawning, of the fish, *Salaria pavo* Risso (Oliveira et al. 2001a). Thus, the connection I found in study IV between high circulating androgen levels and elaborated breeding tubercle ornamentation of male roach is well supported (see also Wiley & Collette 1970).

In the ICHH, the male sexual ornamentation is a handicapping, but honest signal of male quality, due to the high levels of immunosuppressive androgens needed to produce and maintain an effective expression of sexual ornamentation. This is a consequence of either adaptive or nonadaptive immunomodulative action of sex hormones (Wedekind & Folstad 1994, Hillgarth & Wingfield 1997, respectively). In the present study (IV), high levels of circulating testosterone were associated with papillomatosis. This result supports the recent study of Premdas et al. (2001) in which testosterone was found to induce papillomata in *Catostomus commersoni*. In support of my results, some previous studies have shown that high levels of testosterone may be connected to increased parasite infections in the host (e.g. review in Hillgarth & Wingfield 1997, Poiani et al. 2000).

Papillomatosis in fish is induced by stress (e.g. Møllergaard & Nielsen 1995, Premdas et al. 1995) and is found in roach, mainly among males (II). The work by Premdas et al. (2001), in which testosterone implants induced

papillomatosis, or increased the existing papillomata, suggests that testosterone influences a fish's ability to control the infection. In roach, this process may be reinforced by testosterone-induced formation of breeding tubercles. Fast growing organs (breeding tubercles in this case) are particularly vulnerable to tumorigenesis during rapid growth and differentiation (Walter & Israel 1987). However, it can not be ruled out that testosterone would also increase an individual's susceptibility to infection. Nevertheless, the use of papillomatosis in testing the predictions of the ICHH is highly relevant because the male androgen, testosterone contributes the development of the disease. As suggested by many researchers (e.g. Hillgarth & Wingfield 1997, Evans et al. 2000, Poiani et al. 2000), the immunosuppressive mechanism of testosterone during breeding may work together with an increase in circulating cortisol level (see also Slater & Schreck 1993). Results from a recent study with teleosts indicated that cortisol exerted a suppressive effect on leukocyte phagocytosis, but that testosterone or 11-ketotestosterone had no effect (Law et al. 2001). However, testosterone alone was found to elicit significant *in vitro* immunosuppression in anterior kidney leukocytes of chinook salmon (Slater & Schreck 1998). Papillomatosis increases mortality of fishes (Sano et al. 1991). In addition, fish with severe papilloma infection may have an increased risk of secondary fungal or bacterial infections, or of predation. Thus, I propose that spawning papillomatosis disease may give reliable information about a male's intolerance to negative effects of testosterone.

While there was an association between testosterone and disease, I found no relationship between 11-ketotestosterone and papillomatosis. Therefore, in roach, 11-ketotestosterone may work as an androgen that promotes ornament development, but does not increase the risk of papillomatosis. This would provide a means of cheating: males could have elevated 11-ketotestosterone, increased sexual signalling, but would not need to bear the cost of immunosuppression. However, my results indicate that both 11-ketotestosterone and testosterone may be needed to produce breeding tubercles. In addition, 11-ketotestosterone solely has been found to suppress the function of phagocytic cells in another cyprinid, *Cyprinus carpio* L. (Watanuki et al. 2002). Thus, I think that in the present system, the possibility for cheating may be limited. The main defence mechanisms directed against viral infections, in general, include natural killer cells, interferons alpha and beta, specific antibodies and cytotoxic T-lymphocytes (Minton & Sinssons 1992). Therefore, my finding also indicates different relationships of testosterone and 11-ketotestosterone with various parts of the immune system of roach.

The ICHH is probably one of the most controversial recent hypotheses regarding sexual selection. It has given rise to numerous new ideas and studies. The original ICHH predicts that high androgen levels of males should have a positive relationship with sexual ornamentation and a negative relationship with immune defense, leading to increased susceptibility to diseases (Folstad & Karter 1992). However, the variation between individuals in the amount of resources available to invest in ornamentation and immunocompetence makes those relationships difficult to observe at the population level. This is the "big

house, big car problem” which has been recognised in life-history studies (van Noordwijk & de Jong 1986). Nevertheless, in the current study population, a positive connection between sexual ornamentation and testosterone and 11-ketotestosterone was found, as well as a connection between papillomatosis, sexual ornamentation and testosterone, indicating that precisely during the spawning period male roach may have little variation in extra resources to allocate for immune defence.

Interestingly, in study III, I found that the breeding tubercles of wild male roach signalled a long-term resistance to the predominant, harmful trematode parasite, *Rhipidocotyle campanula*, as predicted by the HZH. Since the results of study IV were consistent with the ICHH, to my knowledge, this is the first time when both the ICHH and the HZH processes have been suggested to work simultaneously in the same system. Thus, I propose that, in the present system, the character a male roach signals by his ornamentation may be resistance against parasites (*R. campanula*), and that papillomatosis is an element which contributes to the honesty of the signal. Only high quality male could afford to tolerate the negative effects of testosterone (cf. ICHH), such as increased risk of papillomatosis. In Lake Jyväsjärvi, only 30 percent of high-ornamented males were undiseased (IV).

## 2.7 Breeding tubercles, dominance behaviour and papillomatosis

Success in intrasexual competition may be the main factor determining reproductive outcome in lek-like breeding systems (Andersson 1994, Höglund & Alatalo 1995). A profitable tactic for a male not chosen by female could be to invest more energy in production of badges of status or weapons to aid successful male-male competition (Müller & Ward 1995). Together with evolution of bright ornaments and weaponry, male counter strategies to achieve matings have evolved. In fish species, various reproductive strategies have been found (Oliveira & Almada 1998). Bourgeois (i.e. dominant territory owner) and parasitic roles of males in spawning are alternative mating tactics in fishes. These are not exclusive, however, as bourgeois fish can show opportunistic behaviour (Taborsky 1998). Moreover, sperm competition often has a major role in reproductive output in fishes (Taborsky 1998).

The aim of study V was to test if breeding tubercles act as a status badge indicating male dominance by examining courtship and mating behaviours in pre-spawning events. Furthermore, since papillomatosis is a stress-induced and hormonal-based disease (Premdas et al. 2001; IV), I also studied the presence of epidermal papillomatosis in males and its effect on their behaviour patterns.

In study V I found a clear relationship between the breeding tubercles (skin roughness) and dominance behaviour, indicating that the breeding tubercles may have a signalling role as a status badge in intrasexual selection of roach. By controlling the size of the fish, I could study the signalling role of

breeding tubercles in my experimental system. However, in fishes, the dominance rank has been previously found to increase with age together with size, which has been shown to influence male spawning success in brown trout (Petersson & Järvi 1997). Since no studies have been carried out on the effect of size on dominance, or courting behaviour in roach, I can not estimate how significant that effect is in natural spawning aggregations.

Breeding tubercles are found among several fishes (Wiley & Collette 1970), but their role and function are still uncertain. My results give the first evidence for the significance of breeding tubercles in pre-spawning behaviour of fish. Dominant males had rougher skin than subordinates, so tubercles may work as an intrasexual ornament or status badge. Dominance and the expression of skin tubercles may share the same causal factor, for example, androgens. Nevertheless, the badge of status, in this case breeding tubercles, signals the quality of its bearer. Furthermore, since the breeding tubercles have been shown to indicate parasitic load (Wedekind 1992) and parasite resistance (III), it seems probable that they may function as an ornament of both inter- and intrasexual selection in roach. This does not exclude a partial role for tubercles as a protective organ in spawning (Ahnelt & Keckeis 1994). A status badge may signal good quality to females as well as to males (Berglund et al. 1996) and the present results suggest this to be the case for the breeding tubercles in roach. In the case of secondary sexual traits, male contests very often favor the same signal traits that females prefer (Andersson 1994), which can accelerate the evolution of those traits (Berglund et al. 1996). There are no studies on roach of how the courtship and male dominance are correlated to fitness, but the area is open for future research. In salmon, males showing less quivering and courting behaviour also had lowered reproductive success (Jonsson 1997).

Male roach do not offer clear shelter where they can spawn privately, which increases the possibility of simultaneous parasitic spawning. Therefore, a high dominance rank of a male and the ability to keep other males away from the female probably increases fertilization success. The ability to keep harassing rival males at a distance from the female has been found to be the key variable for breeding success of males in leks of birds (Alatalo et al. 1991).

Interestingly, in the present study papilloma disease did not affect the dominance status of the male. The diseased fish in the trials were able to carry the papillomatosis load and at the same time express their quality with the number and size of the breeding tubercles (cf. Zahavi 1975). Similarly, Hamilton & Poulin (1995) or Barber (2002) could not find any connection between parasitism and dominance in male-male competition. Moreover, the positive relationship between papillomatosis and testosterone found in study IV could explain the current result.

There is evidence of non-random patterns in spawning behaviour in group spawning fish species when spawning behaviours are analyzed in smaller groups (Taborsky 1998). The observed correlation between male dominance status and the breeding tubercle ornamentation in roach provides new insights for studies of lek-mating in cyprinids. Roach is a common iteroparous species having multiple sexual ornaments, which are easily



observed (Wedekind 1992). In addition, it has identifiable skin diseases and known parasites (e.g. Taskinen et al. 1991, II, III). Thus, it offers an ideal system for further studies of sexual selection and lek modelling in fishes.

### 3 CONCLUSIONS

A decrease during spawning in the seasonal pattern of some of the studied immune defence parameters was found (I). Moreover, a novel disease phenomenon of roach, epidermal papillomatosis occurring during the breeding period was described (II). The disease proved to be a common condition in several roach populations. Males had higher prevalence of the disease as did larger fish. Observed gender dependence in the disease prevalence may also reflect differences between sexes in the costs of reproduction. Moreover, the breeding-related seasonal changes in immunocompetence together with an outbreak of papillomatosis during spawning are consistent with the suggested trade-off between reproduction and immune defence. This also suggests that the impact of parasites and pathogens may be notable during the reproductive period. In support of that the prevalence and abundance of gyrodactylid monogenean parasites is also observed to peak in the spring during the spawning period of roach (Koskivaara et al. 1991).

The important finding of this thesis is a remarkable variation between the seasonal patterns of different immunocompetence measures. The seasonal patterns of immune characteristics also differed between populations and sexes. This may indicate a variation in the response of the fish immune system to temporal and spatial environmental changes (including pathogens and parasites). Thus, the present results support the view that the use of any single aspect of immunity as a general measure of immunocompetence is not recommended (Lochmiller 1995, Siva-Jothy 1995, Zuk & Johnsen 1998).

In the third study of my thesis, a positive relationship was found between the proportion of dead *Rhipidocotyle campanula* digenean gill parasites, which is a long-term measure of immunocompetence, and breeding tubercle ornamentation. This is in the line with the HZH, which suggests that sexual ornamentation may reveal to the female a male's resistance against parasites. Due to coevolutionary cycles between host and parasite, the sexual ornamentation may work as a signal of male's resistance to the locally most harmful or abundant parasite in the current system.

Roach male sexual ornamentation, the circulating sexual hormones and spawning papillomatosis form a good model to test the ICHH, since the breeding tubercles are produced by testosterone and 11-ketotestosterone, which may lower the immune defence. Males having higher levels of testosterone and 11-ketotestosterone had a more elaborate ornamentation, but also higher prevalence of papillomatosis (IV). The development of the sexual ornamentation by immunosuppressive androgens may be a handicap, which lowers the immunological status of male and increases the risk of parasites and diseases. Thus, my results in study IV are in line with the predictions of the ICHH.

Since the results of study III were consistent with the HZH, and the results of study IV were consistent with the ICHH, to my knowledge this is the first time that both the ICHH and the HZH processes have been suggested to work simultaneously in the same system. Thus, I propose that, in the present system, the character that a male roach signals by his ornamentation may be resistance against parasites (*R. campanula*), and that spawning papillomatosis is an element which contributes to the honesty of the signal.

In the behavioural trials, the breeding tubercle ornamentation was related to male dominance status (V). Dominance status also correlated with male courtship behaviour. Thus it is possible, that the breeding tubercle ornamentation may work as a status badge for other males, and as a cue to choose a high-quality mate for females. However, interestingly, the papilloma disease did not affect the male dominance status.

To conclude, the pressure from parasites and pathogens may have a remarkable effect on the evolution of teleost life histories and on sexual selection, causing selective processes and even physiological trade-offs between immune defence and other life-history traits.

### *Acknowledgements*

This work is a result of notably intensive working days during 1999-2002. I thank all my friends, my family and all the people at the Department of Biological and Environmental Science of the University of Jyväskylä, including Konnevesi Research Station, for the encouraging support. I thank the Department for providing fine working facilities.

First of all, I am greatly indebted to my supervisor, Jouni Taskinen, who inspired me to study the immunological aspects of life-history strategies. Jouni was my main supervisor, who guided me exhilaratingly into the world of science. I also thank my second supervisor, Ilmari Jokinen. He taught me immunological laboratory techniques. I also thank Tellervo Valtonen who nicely offered me her wide knowledge of parasitology always when it was needed.

Especially I thank Anssi Vainikka for very important share in my study and Markus Rantala for those great endless discussions concerning the billion ways of the evolution in work. I have also to thank my nearest friends, mainly from Kortepohja village: Janne Raunio, Jarno Nevalainen, Jouni Niemelä, Jouni Toivola, Tomi Harjunmaa, Anna Väisänen, Tapio van Ooik, Antti Ellonen, Mikko Känkänen, Tarmo Ketola, Janne Myntti, Jouni Valkonen, Jaakko Tuhkanen, Sami Väänänen, Anna Kaivosari, Janne Kilpimaa and Pauliina Kreivi for good, fair and teaching atmosphere, which made possible my life under stressfull conditions of hard science making.

I thank Janne Myntti, Jarkko Pönkä and Ville Kupari for the assistance in the field. I thank also Lasse Manninen and Ville Sakomaa. I also thank Jani Kupari for the assistance in field and Viivi Raunola for assistance in laboratory. Moreover, I thank Marjatta Kajava who helped organizing the study I.

I would like to thank Rauno Alatalo, Janne Kotiaho, Roger Jones, Markus Rantala and Jari Ahtiainen for valuable criticism and helpful comments on my thesis.

Finally, I am grateful to Emil Aaltonen Foundation for financial support to my thesis. I thank also Rautaruukki group for financial support to the study I. My thesis was conducted in Biological interactions – graduate school of Finnish Ministry of Education.

## YHTEENVETO (Résumé in Finnish)

### Loisten ja taudinaiheuttajien merkitys kalan lisääntymisessä ja seksuaalivalinnassa

Yksi immunologisen ekologian peruskysymyksistä on immuunipuolustuksen rooli elinkierto- ja evoluutioissa, eli mahdollisten kompromissien olemassaolo lisääntymisen ja immunologisen puolustuksen välillä. Tutkin tässä väitöskirjässäni immuunipuolustuksen ja loisresistenssin yhteyttä lisääntymiseen ja seksuaalivalintaan. Mallilajina käytän särkeä (*Rutilus rutilus*).

Immuunipuolustuksen vuodenaikaisvaihtelussa löytyi kutuaikaan kytköksissä olevaa laskua pernan koossa ja etumunuaisen fagosyyttisolujen migraatioaktiivisuudessa, mutta muissa tutkituissa muuttujissa (etumunuais-solujen fagosytointiaktiivisuus, veren IgM-vasta-aine -pitoisuus, valkosolulaskenta ja punasolulaskenta) ei lisääntymiseen liittyviä muutoksia tavattu. Eri immuunipuolustuksen osa-alueilla havaittiin toisistaan eroavat vuodenaikaisrytmit. Lisäksi havaittiin, että kutuaikana särjille puhkeaa papilloomatauti, jota esiintyy huomattavasti useammin koirilla kuin naarilla. Papillooman prevalenssi on korkeampi isoilla kaloilla kuin pienillä kaloilla. Papilloomataudin puhkeaminen voi johtua kutuaikana tapahtuvasta heikentymisestä tietyissä osissa immuunipuolustusta. Tämä antaisi tukea lisääntymisen ja puolustusjärjestelmien välillä olevan kompromissin olemassaololle.

Kenttäaineistossa havaittiin koiraiden pitkän aikavälin loistentappokyvyn ja seksuaaliornamenttina toimivien kutukyhmyjen välillä korrelaatio. Yhteys ornamentointiin havaittiin nimenomaan loisista yleisimmän, *Rhipidocotyle campanula* -imudon puolustuksessa. Löydökset sopivat hyvin yhteen Hamiltonin ja Zukin loisvälitteisen seksuaalivalintateorian kanssa, jossa koiraan seksuaaliornamentit signaloivat vastustuskykyä nimenomaan kulloisenkin ympäristön yleisintä ja haitallisinta loista vastaan. Lisäksi korrelatiivisesta kenttäkokeesta selvisi, että koirassärkien seksuaaliornamentointi, koirassukupuolihormonit ja papilloomatauti ovat voimakkaasti toisiinsa kytköksissä. Voimakkaammin ornementoiduilla koirilla sukupuolihormonitasot olivat korkeammat, mutta niillä oli samanaikaisesti myös enemmän papilloomatautia kuin heikommin ornementoiduilla koirilla. Näyttää siis siltä, että koiralle kutukyhmyjen tuottaminen on kustannus, joka ilmenee kutuaikana immuunipuolustuksen heikkenemisenä ja papilloomatautiriskin kasvamisena. Koiraan kutukyhmyt voisivat olla naaraille rehellinen signaali koiraan laadusta. Edellisestä seuraa, että särjen kohdalla voisi toimia myös seksuaalivalinnan 'immunokompetenssihaitta' -hypoteesi. Tutkimus on ensimmäinen, jossa samassa systeemissä on osoitettu sekä Hamilton-Zukin loisvälitteisen teorian että immunokompetenssihaitta -teorian toimimismahdollisuus.

Käyttäytymiskokeessa selvisi, että hallitseva, dominoiva koira oli useimmiten kutukyhmykseltään karkeampi kuin sen alistettu, subordinaatti

kumppani. Dominantit koirat esittivät myös aktiivisemmin kosiokäyttäytymistä naarasta kohtaan. Papilloomatauti ei kuitenkaan vaikuttanut koiraiden dominanssijärjestykseen.

Yhteenvetona totean, että loisten ja patogeenien merkitys kalojen elinkiertojen evoluutiossa ja seksuaalivalinnassa voi olla huomattava aiheuttaen erilaisia evolutiivisia valintapaineita ja jopa fysiologisia kompromisseja immuunipuolustuksen ja muiden elinkierto-ominaisuuksien kanssa.

**REFERENCES**

- Aaltonen T.M., Jokinen E.I. & Valtonen E.T. 1994. Antibody synthesis in roach (*Rutilus rutilus*); analysis of antibody secreting cells in lymphoid organs with ELISPOT-assay. *Fish and Shellfish Immunology* 4: 129-140.
- Ahnelt H. & Keckeis H. 1994. Breeding tubercles and spawning behaviour in *Chondrostoma nasus* (Teleostei: Cyprinidae): a correlation? *Ichthyological Exploration of Freshwaters* 5: 321-330.
- Alatalo R.V., Höglund J. & Lundberg A. 1991. Lekking in the black grouse - a test of male viability. *Nature* 352: 155-156.
- Andersson M. 1994. *Sexual Selection*. Princeton: Princeton University Press.
- Andersson M. & Iwasa Y. 1996. Sexual selection. *Trends in Ecology and Evolution* 11: 53-58.
- Anderson D.P. & Zeeman G. 1995. Immunotoxicology in fish. In: Rand D.P., (ed.) *Fundamentals of Aquatic Toxicology. Effects, Environmental Fate and Risk Assessment*. Florida: Taylor & Francis. pp. 371-404.
- Avtalion R.R. 1981. Environmental control of the immune response in fish. *Critical Reviews in Environmental Control* 11: 163-168.
- Barber I. 2002. Parasites, male-male competition and female mate choice in the sand goby. *Journal of Fish Biology* 61: 185-198.
- Barber I., Arnott S.A., Braithwaite V.A., Andrew J. & Huntingford F.A. 2001. Indirect fitness consequences of mate choice in sticklebacks: offspring of brighter males grow slowly but resist parasitic infections. *Proceedings of the Royal Society of London B* 268: 71-78.
- Berglund A., Bisazza A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58: 385-399.
- Bolger T. & Connolly P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology* 34: 171-182.
- Borg B. 1994. Androgens in teleost fishes. *Comparative Biochemistry and Physiology C* 109: 219-245.
- Braude S., Tang-Martinez Z. & Taylor G.T. 1999. Stress, testosterone, and the immunoredistribution hypothesis. *Behavioral Ecology* 10: 345-350.
- Buchanan K.L. 2000. Stress and the evolution of condition-dependent signals. *Trends in Ecology and Evolution* 15: 156-160.
- Bylund G., Valtonen E.T. & Niemelä E. 1980. Observations on epidermal papillomata in wild and cultured Atlantic salmon *Salmo salar* L. in Finland. *Journal of Fish Diseases* 3: 525-528.
- Cheek A.O., Thomas P. & Sullivan G.V. 2000. Sex Steroids Relative to Alternative Mating Behaviors in the Simultaneous Hermaphrodite *Serranus subligarius* (Perciformes: Serranidae). *Hormones and Behavior* 37: 189-211.

- Clutton-Brock T.H. & Vincent A.C.J. 1991. Mammalian mating systems. *Nature* 351: 58-60.
- Darwin C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Deerenberg C, Apanius V., Daan S. & Bos N. 1997. Reproductive effort decreases antibody responsiveness. *Proceedings of the Royal Society of London B* 264: 1021-1029.
- Diamond M. 1985. Some observations of spawning by roach, *Rutilus rutilus* L., and bream, *Abramis brama* L., and their implications for management. *Aquaculture and Fisheries Management* 16: 359-367.
- Ebert D. 1994. Virulence and local adaptation of a horizontally transmitted parasite. *Science* 265: 1084-1086.
- Ellis A. 1986. The function of teleost fish lymphocytes in relation to inflammation. *International Journal of Tissue Reactions* 8: 263-270.
- Elofsson U.O.E., Mayer I., Damsgård B. & Wimberg, S. 2000. Intermale Competition in Sexually Mature Arctic Charr: Effects on Brain Monoamines, Endocrine Stress Responses, Sex Hormone Levels, and Behavior. *General and Comparative Endocrinology* 118: 450-460.
- Evans M.R., Goldsmith A.R. & Norris, S.R.A. 2000. The effects of testosterone on antibody production and plumage coloration in male house sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology* 47: 156-163.
- Fisher R.A. 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Folstad I. & Karter A.J. 1992. Parasites, bright males, and the immunocompetence handicap. *The American Naturalist* 139: 603-622.
- Folstad I. & Skarstein F. 1997. Is male germ line control creating avenues for female choice? *Behavioral Ecology* 8: 109-112.
- Gillet C. & Dubois J.P. 1995. A survey of the spawning of perch (*Perca fluviatilis*), pike (*Esox lucius*), and roach (*Rutilus rutilus*), using artificial spawning substrates in lakes. *Hydrobiologia* 300/301: 409-415.
- Hamilton W.D. & Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384-387.
- Hamilton W.J. & Poulin R. 1995. Parasites, aggression and dominance in male upland bullies. *Journal of Fish Biology* 47: 302-307.
- Hamilton W.J. & Poulin R. 1997. The Hamilton and Zuk hypothesis revisited: a meta-analytical approach. *Behaviour* 134: 299-320.
- Hasselquist D., Marsh J.A., Sherman P.W. & Wingfield J.C. 1999. Is avian humoral immunocompetence suppressed by testosterone? *Behavioral Ecology and Sociobiology* 45: 167-175.
- Hillgarth N. & Wingfield J.C. 1997. Parasite-mediated sexual selection: endocrine aspects. In: Clayton D.H., Moore J., (eds) *Host-parasite evolution: general principles and avian models*. Oxford: Oxford University Press, pp. 78-104.
- Hillgarth N., Ramenofsky M. & Wingfield J. 1997. Testosterone and sexual selection. *Behavioral Ecology* 8: 108-109.



- Hoffmann R.W., Körting W., Fischer-Scherl T. & Schäfer W. 1990. An outbreak of bucephalosis in fish of the Main river. *Angewandte Parasitology* 31: 95-99.
- Höglund J. & Alatalo R.V. 1995. *Leks*. Princeton, New Jersey: Princeton University Press.
- Hou Y., Suzuki Y. & Aida K. 1999. Changes in immunoglobulin producing cells in response to gonadal maturation in rainbow trout. *Fisheries Science* 65: 844-849.
- Iida T., Takanishi K. & Wakabayashi H. 1989. Decrease in the bacterial activity of normal serum during the spawning period of rainbow trout. *Bulletin of the Japanese Society of Scientific Fisheries* 55: 463-465.
- Ilmonen P., Taarna T. & Hasselquist D. 2000. Experimentally activated immune defence in female pied flycatchers results in reduced breeding success. *Proceedings of the Royal Society of London B* 267: 665-670.
- Jonsson B. 1997. A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES Journal of Marine Science* 54: 1031-1039.
- Kestemont P., Rinchar J., Feys V. & Fostier A. 1999. Spawning migrations, sexual maturity and sex steroid levels in female roach *Rutilus rutilus* from the River Meuse. *Aquatic Sciences* 61: 111-121.
- Kime D.E. 1998. *Endocrine Disruption in Fish*. London: Kluwer Academic Publishers.
- Kokko H., Brooks R., McNamara J.M. & Houston A.I. 2002. The sexual selection continuum. *Proceedings of the Royal Society of London B*, 269: 1331-1340.
- Koskivaara M., Valtonen E.T. & Prost M. 1991. Seasonal occurrence of gyrodactylid monogeneans on the roach (*Rutilus rutilus*) and variations between four lakes of differing water quality in Finland. *Aqua Fennica* 21: 47-55.
- Kurtz J. & Sauer K.P. 1999. The immunocompetence handicap hypothesis: testing the genetic predictions. *Proceedings of the Royal Society of London B* 266: 2515-2522.
- L'Abée-Lund J.H. & Vøllestad L.A. 1985. Homing precision of roach *Rutilus rutilus* in Lake Årungen, Norway. *Environmental Biology of Fishes* 13: 235-239.
- Law W., Chen W., Song Y., Dufour S. & Chang C. 2001. Differential in Vitro Suppressive Effects of Steroids on Leukocyte Phagocytosis in Two Teleosts, Tilapia and Common Carp. *General and Comparative Endocrinology* 121: 163-172.
- Lee S. & Whitfield P.J. 1992. Virus-associated spawning papillomatosis in smelt, *Osmerus eperlanus* L., in the River Thames. *Journal of Fish Biology* 40: 503-510.
- Liljedal S., Folstad I. & Skarstein F. 1999. Secondary sex traits, parasites, immunity and ejaculate quality in the Arctic charr. *Proceedings of the Royal Society of London B*, 266: 1893-1898.

- Lively C.M. 1999. Migration, virulence, and the geographic mosaic of adaptation by parasites. *The American Naturalist* 153: S34-S47.
- Lochmiller R.L. 1995. Testing the immunocompetence handicap theory. *Trends in Ecology and Evolution* 10: 372-373.
- Lochmiller R.L. & Deerenberg C. 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* 88: 87-98.
- Manning M.J. 1994. Fishes. In: Turner, R.J., (ed.) *Immunology: A comparative approach*. Chichester: John Wiley & Sons Ltd, pp. 69-100.
- Møllergaard S. & Nielsen E. 1995. Impact of oxygen deficiency on the disease status of common dab *Limanda limanda*. *Diseases of the Aquatic Organisms* 22:101-114.
- Mills C.A. 1981. The Spawning of Roach *Rutilus rutilus* (L.) in a Chalk Stream. *Fisheries Management* 12: 49-54.
- Mills C.A. 1991. Reproduction and life history. In: Winfield I.J., Nelson J.S., (eds) *Cyprinid fishes: systematics, biology and exploitation*. London, New York: Chapman & Hall, pp. 483-508.
- Minton J. & Sissons J.G.P. 2000. Viruses, immunity to. In: Flint S.J., Enquist L.W., Krug R.M., Racaniello Y.R., Skalka A.M. (eds) *Principles of Virology Molecular Biology, Pathogenesis, and Control*. Washington DC: ASM Press, pp. 1556-1669.
- Møller A.P. & Alatalo R.V. 1999. Good-genes effects in sexual selection. *Proceedings of the Royal Society of London B* 266: 85-91.
- Møller A.P., Christie P. & Mavarez J. 1998. Condition, disease and immune defense. *Oikos* 83: 301-306.
- Møller A.P., Christie P. & Lux E. 1999. Parasitism, Host Immune Function, and Sexual Selection. *Quarterly Review of Biology* 74: 3-20.
- Møller H. & Anders K. 1986 *Diseases and parasites of marine fishes, Tumors and tumor-like lesions*. Kiel: Verlag Möller, pp. 39-59.
- Müller G. & Ward P. I. 1995. Parasitism and Heterozygosity Influence the Secondary Sexual Characters of the European Minnow, *Phoxinus phoxinus* (L.) (Cyprinidae). *Ethology* 100: 309-319.
- Munkittrick K.R. & Leatherland J.F. 1982. Haematocrit values in feral goldfish, *Carassius auratus* L., as indicators of the health of the population. *Journal of Fish Biology* 23: 153-161.
- Nelson R.D., Quie P.G. & Simmons R.L. 1975. Chemotaxis under agarose: a new and simple method for measuring chemotaxis and spontaneous migration of human polymorphonuclear leukocytes and monocytes. *Journal of Immunology* 115: 1650-1656.
- Nelson R.J. & Demas G.E. 1996. Seasonal changes in immune function. *Quarterly Review of Biology* 71: 511-548.
- van Noordwijk A.J. & de Jong G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist* 128: 137-142.
- Nordling D., Andersson M., Zohari S. & Gustafsson L. 1998 Reproductive effort reduces specific immune response and parasite resistance. *Proceedings of the Royal Society of London B* 265: 1291-1298.

- Norris K. & Evans M.R. 2000. Ecological immunology: life history trade-offs and immune defense in birds. *Behavioral Ecology* 11: 19-26.
- Oliveira R.F. & Almada V.C. 1998. Mating tactics and male-male courtship in the lek-breeding cichlid *Oreocromis mossambicus*. *Journal of Fish Biology* 52: 1115-1129.
- Oliveira R.F., Almada V.C., Goncalves E.J., Forsgren E. & Canario, A.V.M. 2001a. Androgen levels and social interactions in breeding males of the peacock blenny. *Journal of Fish Biology* 58: 897-908.
- Oliveira R.F., Canario A.V.M., Grober M.S. & Santos R.S. 2001b. Endocrine Correlates of Male Polymorphism and Alternative Reproductive Tactics in the Azorean Rock-Pool Blenny, *Parablennius sanguinolentus parvicornis*. *General and Comparative Endocrinology* 121: 278-288.
- Penn D. & Potts W.K. 1998. Chemical signals and parasite-mediated sexual selection. *Trends in Ecology and Evolution* 13: 391-396.
- Peters A. 2000. Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent. *Proceedings of the Royal Society of London B* 267: 883-889.
- Petersson E., Järvi T., Olsens H., Mayer I. & Hedenskog M. 1999. Male-male competition and female choice in brown trout. *Animal Behavior* 57: 777-783.
- Piersma T. & Lindström Å. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends in Ecology and Evolution* 12: 134-138.
- Pomiankowski A. & Iwasa Y. 1998. Runaway ornament diversity caused by Fisherian sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* 95: 5106-5111.
- Poiani A., Goldsmith A.R. & Evans M.R. 2000. Ectoparasites of house sparrows (*Passer domesticus*): an experimental test of the immunocompetence handicap hypothesis and a new model. *Behavioral Ecology and Sociobiology* 47: 230-242.
- Pottinger T.G. & Carrick T.R. 2000. Contrasting seasonal modulation of the stress response in male and female rainbow trout. *Journal of Fish Biology* 56: 667-675.
- Poncin P., Philippart J.C. & Ruwet J.C. 1996. Territorial and non-territorial spawning behaviour in the bream. *Journal of Fish Biology* 49: 622-626.
- Premdas P.D., Metcalfe T.L., Bailey M.E. & Metcalfe C.D. 1995. The prevalence and histological appearance of lip papillomas in white suckers (I) from two sites in central Ontario, Canada. *Journal Great Lakes Research* 21: 207-219.
- Premdas P.D., Metcalfe C.D. & Brown S. 2001. The effects of 17 $\alpha$ -oestradiol, testosterone and tamoxifen on the development of papillomata in *Catostomus commersoni*. *Journal of Fish Biology* 59: 1056-1069.
- Råberg L., Grahn M., Hasselquist D. & Svensson E. 1998. On the adaptive significance of stress-induced immunosuppression. *Proceedings of the Royal Society of London B* 265: 1637-1641.

- Rantala M.J. & Kortet R. 2002. Courtship song and immune function in the field cricket *Gryllus bimaculatus*. *Biological Journal of the Linnean Society*, conditionally accepted for publication.
- Rantala M.J., Jokinen I., Kortet R. & Vainikka A., Suhonen J. 2002. Do pheromones reveal male immunocompetence? *Proceedings of the Royal Society of London B* 269: 1681-1685.
- Rinchart J., Kestemont P. & Heine R. 1997. Comparative study of reproductive biology in single and multiple-spawner cyprinid fish. II. Sex steroid and plasma protein phosphorus concentrations. *Journal of Fish Biology* 50: 169-180.
- Roff D.A. 1992. *The Evolution of Life Histories*. Routledge: Chapman & Hall, Inc.
- Saino N., Bolzern A.M. & Møller A.P. 1997. Immunocompetence, ornamentation, and viability of male barn swallows (*Hirundo rustica*). *Proceedings of the National Academy of Sciences of the United States of America* 94: 549-552.
- Sano T., Morita N., Shima N. & Akimoto M. 1991. Herpesvirus cyprini: lethality and oncogenicity. *Journal of Fish Diseases* 14: 533-543.
- Salo H.M., Aaltonen T.A., Markkula E. & Jokinen E.I. 1998. Ultraviolet B Irradiation Modulates the Immune System of Fish (*Rutilus rutilus*, Cyprinidae). I. Phagocytes. *Photochemistry and Photobiology* 67: 433-437.
- Salo H.M., Jokinen E.I., Markkula S.E. & Aaltonen T.M. 2000. Ultraviolet B Irradiation Modulates the Immune System of Fish (*Rutilus rutilus*, Cyprinidae) II: Blood. *Photochemistry and Photobiology* 71: 65-70.
- Secombes C. 1996. The nonspecific immune system: Cellular defences. In: Iwama G., Nakanishi T., (eds) *The Fish Immune System: Organism, Pathogen and Environment*. San Diego: Academic Press, pp. 43-103.
- Secombes C.J. & Fletcher T.C. 1992. The role of phagocytes in the protective mechanisms of fish. *Annual Review of Fish Diseases* 2: 53-71.
- Scott A.L. & Klesius P.H. 1981. Chemiluminescence: a novel analysis of phagocytosis in fish. *Development in Biological Standardisation* 49: 243-254.
- Shaw A.F.B. 1930. A direct method for counting the leucocytes, thrombocytes and erythrocytes of birds's blood. *Journal of Pathology and Bacteriology* 33: 833-835.
- Sheldon B.C. & Verhulst S. 1996. Ecological Immunology: costly parasite defence and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution* 11: 317-321.
- Siva-Jothy M.T. 1995. 'Immunocompetence': conspicuous by its absence. *Trends in Ecology and Evolution* 10: 205-206.
- Skarstein F. & Folstad I. 1996. Sexual dichromatism and the immunocompetence handicap: an observational approach using arctic charr. *Oikos* 76: 359-367.

- Skarstein F., Folstad I. & Liljedal S. 2001. Whether to reproduce or not: immune suppression and cost of parasites during reproduction in the Arctic charr. *Canadian Journal of Zoology* 79: 271-278.
- Slater C.H. & Schreck C.B. 1993. Testosterone Alters the Immune Response of Chinook Salmon, *Onchorhynchus tshawytscha*. *General and Comparative Endocrinology* 89: 291-298.
- Slater C.H. & Schreck C.B. 1998. Season and physiological parameters modulate salmonid leucocyte androgen receptor affinity and abundance. *Fish and Shellfish Immunology* 8: 379-391.
- Spivak E.G., Pinus G.N. & Sentishcheva S.V. 1979. The Age Composition of the Spawning Population and the Characteristics of the Spawners Size-Age Structure and Fecundity of the Roach, *Rutilus rutilus* Spawning in Kakhovka Reservoir. *Journal of Ichthyology* 19:75-80.
- Stearns S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Svärdson G. 1951. Spawning behaviour of *Leuciscus rutilus* (Linné). *Reports of the Institute of Freshwater Research, Drottningholm* 33: 199-203.
- Taborsky M. 1998. Sperm competition in fish: 'bourgeois' males and parasitic spawning. *Trends in Ecology and Evolution* 13: 222-227.
- Taskinen J., Valtonen E.T. & Gibson D.I. 1991. Studies on bucephalid digeneans parasitising molluscs and fishes in Finland. I. Ecological data and experimental studies. *Systematics Parasitology* 19: 81-94.
- Tatner M.F. 1996. Natural Changes in the Immune System of Fish. In: Iwama G, Nakanishi T, (eds) *The Fish Immune System: Organism, Pathogen, and Environment*. San Diego: Academic Press Inc., pp. 255-288.
- Verhulst S., Dieleman S.J. & Parmentier H.K. 1999. A tradeoff between immunocompetence and sexual ornamentation in domestic fowl. *Proceedings of the National Academy of Sciences of the United States of America* 96: 4478-4481.
- Vladykov V.D., Renaud C.B. & Laframboise S. 1985. Breeding tubercles in three species of *Gadus* (cods). *Canadian Journal of Fisheries and Aquatic Sciences* 42: 608-615.
- Vøllestad L.A. & L'Abée-Lund J.H. 1987. Reproductive biology of stream-spawning roach, *Rutilus rutilus*. *Environmental Biology of Fishes* 18: 219-227.
- Walter J.B. & Israel M.S. 1987. *General Pathology*. New York: Churchill Livingstone.
- Watanuki H., Yamaguchi T. & Sakai M. 2002. Suppression in function of phagocytic cells in common carp *Cyprinus carpio* L. injected with estradiol, progesterone or 11-ketotestosterone.
- Wedekind C. 1992. Detailed information about parasites revealed by sexual ornamentation. *Proceedings of the Royal Society of London B* 204: 169-174.
- Wedekind C. 1996. Lek-like spawning behaviour and different female mate preferences in roach (*Rutilus rutilus*). *Behaviour* 133: 681-695.

- Wedekind C. & Folstad I. 1994. Adaptive or nonadaptive immunosuppression by sex hormones? *The American Naturalist* 143: 936-938.
- Wedekind C., Müller R. & Spicher H. 2001. Potential genetic benefits of mate selection in whitefish. *Journal of Evolutionary Biology* 14: 980-986.
- Wester P.W., Vethaak A.D. & van Muiswinkel W.B. 1994. Fish Biomarkers in immunotoxicology. *Toxicology* 86: 213-232.
- Westneat D.F. & Birkhead T.R. 1998. Alternative hypotheses linking the immune system and mate choice for good genes. *Proceedings of the Royal Society of London B* 265: 1065-1073.
- Wiley M.L. & Collette B.B. 1970. Breeding tubercles and contact organs in fishes: their occurrence, structure, and significance. *Bulletin of the American Museum of Natural History* 143: 145-216.
- Wootton, R.J. 1990. *Ecology of Teleost Fishes*. London: Chapman & Hall.
- Zahavi A. 1975. Mate selection - a selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.
- Zahavi A. 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* 67: 603-605.
- Zapata A.G. & Cooper E.L. 1990. *The Immune System: Comparative Histophysiology*. Chichester: John Wiley & Sons Ltd.
- Zapata A.G., Varas A. & Torroba M. 1992. Seasonal variations in the immune system of lower vertebrates. *Immunology Today* 13: 142-147.
- Zuk M. & Johnsen T.S. 1998. Seasonal changes in the relationship between ornamentation and immune response in red jungle fowl. *Proceedings of the Royal Society of London B* 265: 1631-1635.

BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

- 1 RAATIKAINEN, M. & VASARAINEN, A., Damage caused by timothy flies (*Amaurosoma* spp.) in Finland, pp. 3-8.  
SÄRKKÄ, J., The numbers of *Tubifex tubifex* and its cocoons in relation to the mesh size, pp. 9-13.  
ELORANTA, P. & ELORANTA, A., Keurusselän kalastosta ja sen rakenteesta. - On the fish fauna of Lake Keurusselkä, Finnish Lake District, pp. 14-29.  
ELORANTA, P. & ELORANTA, A., Kuusveden veden laadusta, kasviplanktonista ja kalastosta. - On the properties of water, phytoplankton and fish fauna of Lake Kuusvesi, Central Finland, pp. 30-47. 47 p. 1975.
- 2 ELORANTA, V., Effects of different process wastes and main sewer effluents from pulp mills on the growth and production of *Ankistrodesmus falcatus* var. *acicularis* (Chlorophyta), pp. 3-33.  
ELORANTA, P. & KUNNAS, S., A comparison of littoral periphyton in some lakes of Central Finland, pp. 34-50.  
ELORANTA, P., Phytoplankton and primary production in situ in the lakes Jyväsjärvi and North Päijänne in summer 1974, pp. 51-66. 66 p. 1976.
- 3 RAATIKAINEN, M., HALKKA, O., VASARAINEN, A. & HALKKA, L., Abundance of *Philaenus spumarius* in relation to types of plant community in the Tvärminne archipelago, southern Finland. 38 p. 1977
- 4 HAKKARI, L., On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland. 87 p. 1978.
- 5 KÄPYLÄ, M., Bionomics of five woodnesting solitary species of bees (Hym., Megachilidae), with emphasis on flower relationships. 89 p. 1978.
- 6 KANKAALA, P. & SAARI, V., The vascular flora of the Vaarunvuoret hills and its conservation, pp. 3-62.  
TÖRMÄLÄ, T. & KOVANEN, J., Growth and ageing of magpie (*Pica pica* L.) nestlings, pp. 63-77. 77 p. 1979.
- 7 VIITALA, J., Hair growth patterns in the vole *Clethrionomys rufocanus* (Sund.), pp. 3-17.  
NIEMI, R. & HUHTA, V., Oribatid communities in artificial soil made of sewage sludge and crushed bark, pp. 18-30. 30 p. 1981.
- 8 TÖRMÄLÄ, T., Structure and dynamics of reserved field ecosystem in central Finland. 58 p. 1981.
- 9 ELORANTA, V. & KUIVASNIEMI, K., Acute toxicity of two herbicides, glyphosate and 2,4-D, to *Selenastrum capricornutum* Printz (Chlorophyta), pp. 3-18.  
ELORANTA, P. & KUNNAS, S., Periphyton accumulation and diatom communities on artificial substrates in recipients of pulp mill effluents, pp. 19-33.  
ELORANTA, P. & MARJA-AHO, J., Transect studies on the aquatic macrophyte vegetation of Lake Saimaa in 1980, pp. 35-65. 65 p. 1982.
- 10 LAKE PÄIJÄNNE SYMPOSIUM. 199 p. 1987.
- 11 SAARI, V. & OHENOJA, E., A check-list of the larger fungi of Central Finland. 74 p. 1988.
- 12 KOJOLA, I., Maternal investment in semi-domesticated reindeer (*Rangifer t. tarandus* L.). 26 p. *Yhteenveto* 2 p. 1989.
- 13 MERILÄINEN, J. J., Impact of an acid, polyhumic river on estuarine zoobenthos and vegetation in the Baltic Sea, Finland. 48 p. *Yhteenveto* 2 p. 1989.
- 14 LUMME, I., On the clone selection, ectomy-corrhizal inoculation of short-rotation willows (*Salix* spp.) and on the effects of some nutrients sources on soil properties and plant nutrition. 55 p. *Yhteenveto* 3 p. 1989.
- 15 KUITUNEN, M., Food, space and time constraints on reproduction in the common treecreeper (*Certhia familiaris* L.) 22 p. *Yhteenveto* 2 p. 1989.
- 16 YLÖNEN, H., Temporal variation of behavioural and demographical processes in cyclic *Clethrionomys* populations. 35 p. *Yhteenveto* 2 p. 1989.
- 17 MIKKONEN, A., Occurrence and properties of proteolytic enzymes in germinating legume seeds. 61 p. *Yhteenveto* 1 p. 1990.
- 18 KAINULAINEN, H., Effects of chronic exercise and ageing on regional energy metabolism in heart muscle. 76 p. *Yhteenveto* 1 p. 1990.
- 19 LAKSO, MERJA, Sex-specific mouse testosterone 16 $\alpha$ -hydroxylase (cytochrome P450) genes: characterization and genetic and hormonal regulations. 70 p. *Yhteenveto* 1 p. 1990.
- 20 SETÄLÄ, HEIKKI, Effects of soil fauna on decomposition and nutrient dynamics in coniferous forest soil. 56 p. *Yhteenveto* 2 p. 1990.
- 21 NÄRVÄNEN, ALE, Synthetic peptides as probes for protein interactions and as antigenic epitopes. 90 p. *Yhteenveto* 2 p. 1990.
- 22 ECOTOXICOLOGY SEMINAR, 115 p. 1991.
- 23 ROSSI, ESKO, An index method for environmental risk assessment in wood processing industry. 117 p. *Yhteenveto* 2 p. 1991.
- 24 SUHONEN, JUKKA, Predation risk and competition in mixed species tit flocks. 29 p. *Yhteenveto* 2 p. 1991.
- 25 SUOMEN MUUTTAVA LUONTO. Mikko Raatikaiselle omistettu juhla-kirja. 185 p. 1992.
- 26 KOSKIVAARA, MARI, Monogeneans and other parasites on the gills of roach (*Rutilus rutilus*) in Central Finland. Differences between four lakes and the nature of dactylogyrid communities. 30 p. *Yhteenveto* 2 p. 1992.
- 27 TASKINEN, JOUNI, On the ecology of two Rhipidocotyle species (Digenea: Bucephalidae) from two Finnish lakes. 31 p. *Yhteenveto* 2 p. 1992.
- 28 HUOVILA, ARI, Assembly of hepatitis B surface antigen. 73 p. *Yhteenveto* 1 p. 1992.
- 29 SALONEN, VEIKKO, Plant colonization of harvested peat surfaces. 29 p. *Yhteenveto* 2 p. 1992.

BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

- 30 JOKINEN, ILMARI, Immunoglobulin production by cultured lymphocytes of patients with rheumatoid arthritis: association with disease severity. 78 p. Yhteenveto 2 p. 1992.
- 31 PUNNONEN, Eeva-Liisa, Ultrastructural studies on cellular autophagy. Structure of limiting membranes and route of enzyme delivery. 77 p. Yhteenveto 2 p. 1993.
- 32 HAIMI, JARI, Effects of earthworms on soil processes in coniferous forest soil. 35 p. Yhteenveto 2 p. 1993.
- 33 ZHAO, GUOCHANG, Ultraviolet radiation induced oxidative stress in cultured human skin fibroblasts and antioxidant protection. 86 p. Yhteenveto 1 p. 1993.
- 34 RÄTTI, OSMO, Polyterritorial polygyny in the pied flycatcher. 31 p. Yhteenveto 2 p. 1993.
- 35 MARIOMÄKI, VARPU, Endosomes and lysosomes in cardiomyocytes. A study on morphology and function. 64 p. Yhteenveto 1 p. 1993.
- 36 KIHILSTRÖM, MARKKU, Myocardial antioxidant enzyme systems in physical exercise and tissue damage. 99 p. Yhteenveto 2 p. 1994.
- 37 MUOTKA, TIMO, Patterns in northern stream guilds and communities. 24 p. Yhteenveto 2 p. 1994.
- 38 EFFECT OF FERTILIZATION ON FOREST ECOSYSTEM 218 p. 1994.
- 39 KERVINEN, JUKKA, Occurrence, catalytic properties, intracellular localization and structure of barley aspartic proteinase. 65 p. Yhteenveto 1 p. 1994.
- 40 MAPPES, JOHANNA, Maternal care and reproductive tactics in shield bugs. 30 p. Yhteenveto 3 p. 1994.
- 41 SIKAMÄKI, PIIRKKO, Determinants of clutch-size and reproductive success in the pied flycatcher. 35 p. Yhteenveto 2 p. 1995.
- 42 MAPPES, TAPIO, Breeding tactics and reproductive success in the bank vole. 28 p. Yhteenveto 3 p. 1995.
- 43 LAITINEN, MARKKU, Biomonitoring of the responses of fish to environmental stress. 39 p. Yhteenveto 2 p. 1995.
- 44 LAPPALAINEN, PEKKA, The dinuclear Cu<sub>2</sub> centre of cytochrome oxidase. 52 p. Yhteenveto 1 p. 1995.
- 45 RINTAMÄKI, PEKKA, Male mating success and female choice in the lekking black grouse. 23 p. Yhteenveto 2 p. 1995.
- 46 SUURONEN, TIINA, The relationship of oxidative and glycolytic capacity of longissimus dorsi muscle to meat quality when different pig breeds and crossbreeds are compared. 112 p. Yhteenveto 2 p. 1995.
- 47 KOSKENNIEMI, ESA, The ecological succession and characteristics in small Finnish polyhumic reservoirs. 36 p. Yhteenveto 1 p. 1995.
- 48 HOVI, MATTI, The lek mating system in the black grouse: the role of sexual selection. 30 p. Yhteenveto 1 p. 1995.
- 49 MARTTILA, SALLA, Differential expression of aspartic and cyteine proteinases, glutamine synthetase, and a stress protein, HVA1, in germinating barley. 54 p. Yhteenveto 1 p. 1996.
- 50 HUHTA, ESA, Effects of forest fragmentation on reproductive success of birds in boreal forests. 26 p. Yhteenveto 2 p. 1996.
- 51 OJALA, JOHANNA, Muscle cell differentiation in vitro and effects of antisense oligodeoxyribonucleotides on gene expression of contractile proteins. 157 p. Yhteenveto 2 p. 1996.
- 52 PALOMÄKI, RISTO, Biomass and diversity of macrozoobenthos in the lake littoral in relation to environmental characteristics. 27 p. Yhteenveto 2 p. 1996.
- 53 PUSENIUS, JYRKI, Intraspecific interactions, space use and reproductive success in the field vole. 28 p. Yhteenveto 2 p. 1996.
- 54 SALMINEN, JANNE, Effects of harmful chemicals on soil animal communities and decomposition. 28 p. Yhteenveto 2 p. 1996.
- 55 KOTIAHO, JANNE, Sexual selection and costs of sexual signalling in a wolf spider. 25 p. (96 p.). Yhteenveto 2 p. 1997.
- 56 KOSKELA, JUHA, Feed intake and growth variability in Salmonids. 27p. (108 p.). Yhteenveto 2 p. 1997.
- 57 NAARALA, JONNE, Studies in the mechanisms of lead neurotoxicity and oxidative stress in human neuroblastoma cells. 68 p. (126 p.). Yhteenveto 1 p. 1997.
- 58 AHO, TEIJA, Determinants of breeding performance of the Eurasian tree creeper. 27 p. (130 p.). Yhteenveto 2 p. 1997.
- 59 HAAPARANTA, AHTI, Cell and tissue changes in perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in relation to water quality. 43 p. (112 p.). Yhteenveto 3 p. 1997.
- 60 SOIMASUO, MARKUS, The effects of pulp and paper mill effluents on fish: a biomarker approach. 59 p. (158 p.). Yhteenveto 2 p. 1997.
- 61 MIKOLA, JUHA, Trophic-level dynamics in microbial-based soil food webs. 31 p. (110 p.). Yhteenveto 1 p. 1997.
- 62 RAHKONEN, RIITTA, Interactions between a gull tapeworm *Diphyllobothrium dendriticum* (Cestoda) and trout (*Salmo trutta* L.). 43 p. (69 p.). Yhteenveto 3 p. 1998.
- 63 KOSKELA, ESA, Reproductive trade-offs in the bank vole. 29 p. (94 p.). Yhteenveto 2 p. 1998.
- 64 HORNE, TAINA, Evolution of female choice in the bank vole. 22 p. (78 p.). Yhteenveto 2 p. 1998.
- 65 PIIRHONEN, JUHANI, Some effects of cultivation on the smolting of two forms of brown trout (*Salmo trutta*). 37 p. (97 p.). Yhteenveto 2 p. 1998.
- 66 LAAKSO, JOUNI, Sensitivity of ecosystem functioning to changes in the structure of soil food webs. 28 p. (151 p.). Yhteenveto 1 p. 1998.
- 67 NIKULA, TUOMO, Development of radiolabeled monoclonal antibody constructs: capable of transporting high radiation dose into cancer cells. 45 p. (109 p.). Yhteenveto 1 p. 1998.



## BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

- 68 AIRENNE, KARI, Production of recombinant avidins in *Escherichia coli* and insect cells. 96 p. (136 p.). Yhteenveto 2 p. 1998.
- 69 LYYTIKÄINEN, TAPANI, Thermal biology of underyearling Lake Inari Arctic Charr *Salvelinus alpinus*. 34 p. (92 p.). Yhteenveto 1 p. 1998.
- 70 VIHINEN-RANTA, MAIJA, Canine parvovirus. Endocytic entry and nuclear import. 74 p. (96 p.). Yhteenveto 1 p. 1998.
- 71 MARTIKAINEN, ESKO, Environmental factors influencing effects of chemicals on soil animals. Studies at population and community levels. 44 p. (137 p.). Yhteenveto 1 p. 1998.
- 72 AHLROTH, PETRI, Dispersal and life-history differences between waterstrider (*Aquarius najas*) populations. 36 p. (98 p.). Yhteenveto 1 p. 1999.
- 73 SIPPONEN, MATTI, The Finnish inland fisheries system. The outcomes of private ownership of fishing rights and of changes in administrative practices. 81 p. (188 p.). Yhteenveto 2 p. 1999.
- 74 LAMMI, ANTTI, Reproductive success, local adaptation and genetic diversity in small plant populations. 36 p. (107 p.). Yhteenveto 4 p. 1999.
- 75 NIVA, TEUVO, Ecology of stocked brown trout in boreal lakes. 26 p. (102 p.). Yhteenveto 1 p. 1999.
- 76 PULKKINEN, KATJA, Transmission of *Triaenophorus crassus* from copepod first to coregonid second intermediate hosts and effects on intermediate hosts. 45 p. (123 p.). Yhteenveto 3 p. 1999.
- 77 PARRI, SILJA, Female choice for male drumming characteristics in the wolf spider *Hygrolycosa rubrofasciata*. 34 p. (108 p.). Yhteenveto 2 p. 1999.

## JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 78 VIROLAINEN, KAIJA, Selection of nature reserve networks. - Luonnonsuojelualueiden valinta. 28 p. (87 p.). Yhteenveto 1 p. 1999.
- 79 SELIN, PIRKKO, Turvevarojen teollinen käyttö ja suopohjan hyödyntäminen Suomessa. - Industrial use of peatlands and the re-use of cut-away areas in Finland. 262 p. Foreword 3 p. Executive summary 9 p. 1999.
- 80 LEPPÄNEN, HARRI, The fate of resin acids and resin acid-derived compounds in aquatic environment contaminated by chemical wood industry. - Hartsihappojen ja hartsihappoppe- räisten yhdisteiden ympäristökohtalo kemiallisen puunjalostusteollisuuden likaamissa vesistöissä. 45 p. (149 p.). Yhteenveto 2 p. 1999.
- 81 LINDSTRÖM, LEENA, Evolution of conspicuous warning signals. - Näkyvien varoitussignaalien evoluutio. 44 p. (96 p.). Yhteenveto 3 p. 2000.
- 82 MATTILA, ELISA, Factors limiting reproductive success in terrestrial orchids. - Kämmeköiden lisääntymismenestystä rajoittavat tekijät. 29 p. (95 p.). Yhteenveto 2 p. 2000.
- 83 KARELS, AARNO, Ecotoxicity of pulp and paper mill effluents in fish. Responses at biochemical, individual, population and community levels. - Sellu- ja paperiteollisuuden jätevesien ekotoksisuus kaloille. Tutkimus kalojen biokemiallisista, fysiologisista sekä populaatio- ja yhteisövasteista. 68 p. (177 p.). Yhteenveto 1 p. Samenvatting 1 p. 2000.
- 84 AALTONEN, TUULA, Effects of pulp and paper mill effluents on fish immune defence. - Met- säteellisuuden jätevesien aiheuttamat immunologiset muutokset kaloissa. 62 p. (125 p.). 2000.
- 85 HELENIUS, MERJA, Aging-associated changes in NF-kappa B signaling. - Ikääntymisen vaikutus NF-kappa B:n signalointiin. 75 p. (143 p.). Yhteenveto 2 p. 2000.
- 86 HUOVINEN, PIRJO, Ultraviolet radiation in aquatic environments. Underwater UV penetration and responses in algae and zooplankton. - Ultraviolet säteilyn vedenalain- nen tunkeutuminen ja sen vaikutukset leviin ja eläinplanktoniin. 52 p. (145 p.). Yhteenveto 2 p. 2000.
- 87 PÄÄKKÖNEN, JARI-PEKKA, Feeding biology of burbot, *Lota lota* (L.): Adaptation to profundal lifestyle? - Mateen, *Lota lota* (L), ravinnon- käytön erityispiirteet: sopeumia pohja- elämään? 33 p. (79 p.). Yhteenveto 2 p. 2000.
- 88 LAASONEN, PEKKA, The effects of stream habit restoration on benthic communities in boreal headwater streams. - Koskikunnostuksen vaikutus jokien pohjaeläimistöön. 32 p. (101 p.). Yhteenveto 2 p. 2000.
- 89 PASONEN, HANNA-LEENA, Pollen competition in silver birch (*Betula pendula* Roth). An evolutionary perspective and implications for commercial seed production. - Siitepölykilpailu koivulla. 41 p. (115 p.). Yhteenveto 2 p. 2000.
- 90 SALMINEN, ESA, Anaerobic digestion of solid poultry slaughterhouse by-products and wastes. - Siipikarjateurastuksen sivutuotteiden ja jätteiden anaerobinen käsittely. 60 p. (166 p.). Yhteenveto 2 p. 2000.
- 91 SALO, HARRI, Effects of ultraviolet radiation on the immune system of fish. - Ultravioletti- säteilyn vaikutus kalan immunologiseen puolustusjärjestelmään. 61 p. (109 p.). Yhteenveto 2 p. 2000.
- 92 MUSTAJÄRVI, KAISA, Genetic and ecological consequences of small population size in *Lychnis viscaria*. - Geneettisten ja ekologisten tekijöiden vaikutus pienten mäkitervakko- populaatioiden elinkykyyn. 33 p. (124 p.). Yhteenveto 3 p. 2000.

JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 93 TIKKA, PÄIVI, Threatened flora of semi-natural grasslands: preservation and restoration. - Niittykasvillisuuden säilyttäminen ja ennallistaminen. 35 p. (105 p.). Yhteenveto 2 p. 2001.
- 94 SIITARI, HELI, Ultraviolet sensitivity in birds: consequences on foraging and mate choice. - Lintujen ultravioletin ekologinen merkitys ravinnon- ja puolisonvalinnassa. 31 p. (90 p.). Yhteenveto 2 p. 2001.
- 95 VERTAINEN, LAURA, Variation in life-history traits and behaviour among wolf spider (*Hygrolycosa rubrofasciata*) populations. - Populaatioiden väliset erot rummuttavan hämähäkin *Hygrolycosa rubrofasciata* kasvu- ja käyttäytymisessä. 37 p. (117 p.) Yhteenveto 2 p. 2001.
- 96 HAAPALA, ANTTI, The importance of particulate organic matter to invertebrate communities of boreal woodland streams. Implications for stream restoration. - Hiukkasmaisen orgaanisen aineksen merkitys pohjoisten metsäjokien pohja-eläinyhteisölle - huomioita virtavesien kunnostushankkeisiin. 35 p. (127 p.) Yhteenveto 2 p. 2001.
- 97 NISSINEN, LIISA, The collagen receptor integrins - differential regulation of their expression and signaling functions. - Kollageeniin sitoutuvat integriinit - niiden toisistaan eroava säätely ja signaali. 67 p. (125 p.) Yhteenveto 1 p. 2001.
- 98 AHLROTH, MERVI, The chicken avidin gene family. Organization, evolution and frequent recombination. - Kanan avidiini-geeniperhe. Organisaatio, evoluutio ja tiheä rekombinaatio. 73 p. (120 p.) Yhteenveto 2 p. 2001.
- 99 HYÖTYLÄINEN, TARJA, Assessment of ecotoxicological effects of creosote-contaminated lake sediment and its remediation. - Kreosotilla saastuneen järvisedimentin ekotoksikologisen riskin ja kunnostuksen arviointi. 59 p. (132 p.) Yhteenveto 2 p. 2001.
- 100 SULKAVA, PEKKA, Interactions between faunal community and decomposition processes in relation to microclimate and heterogeneity in boreal forest soil. - Maaperän eliöyhteisön ja hajotusprosessien väliset vuorovaikutukset suhteessa mikroilmastoon ja laikutaisuuteen. 36 p. (94 p.) Yhteenveto 2 p. 2001.
- 101 LAITINEN, OLLI, Engineering of physicochemical properties and quaternary structure assemblies of avidin and streptavidin, and characterization of avidin related proteins. - Avidiinin ja streptavidiinin kvaternäärirakenteen ja fysiokeemiallisten ominaisuuksien muokkaus sekä avidiinin kaltaisten proteiinien karakterisointi. 81 p. (126 p.) Yhteenveto 2 p. 2001.
- 102 LYYTINEN, ANNE, Insect coloration as a defence mechanism against visually hunting predators. - Hyönteisten väritys puolustuksessa vihollisia vastaan. 44 p. (92 p.) Yhteenveto 3 p. 2001.
- 103 NIKKILÄ, ANNA, Effects of organic material on the bioavailability, toxicokinetics and toxicity of xenobiotics in freshwater organisms. - Orgaanisen aineksen vaikutus vierasainoiden biosaatavuuteen, toksikokinetiikkaan ja toksisuuteen vesieliöillä. 49 p. (102 p.) Yhteenveto 3 p. 2001.
- 104 LIIRI, MIRA, Complexity of soil faunal communities in relation to ecosystem functioning in coniferous forest soil. A disturbance oriented study. - Maaperän hajottajaeliöstön monimuotoisuuden merkitys metsäekosysteemin toiminnassa ja häiriötilanteissa. 36 p. (121 p.) Yhteenveto 2 p. 2001.
- 105 KOSKELA, TANJA, Potential for coevolution in a host plant - holoparasitic plant interaction. - Isäntäkasvin ja täysloiskasvin välinen vuorovaikutus: edellytyksiä koevoluutiolle? 44 p. (122 p.) Yhteenveto 3 p. 2001.
- 106 LAPPIVAARA, JARMO, Modifications of acute physiological stress response in whitefish after prolonged exposures to water of anthropogenically impaired quality. - Ihmistoiminnan aiheuttaman veden laadun heikentymisen vaikutukset planktonsiian fysiologisessa stressivasteessa. 46 p. (108 p.) Yhteenveto 3 p. 2001.
- 107 ECCARD, JANA, Effects of competition and seasonality on life history traits of bank voles. - Kilpailun ja vuodenaikavaihtelun vaikutus metsämyyrän elinkiertoosiin. 29 p. (115 p.) Yhteenveto 2 p. 2002.
- 108 NIEMINEN, JOUNI, Modelling the functioning of experimental soil food webs. - Kokeellisten maaperäravintoverkkojen toiminnan mallintaminen. 31 p. (111 p.) Yhteenveto 2 p. 2002.
- 109 NYKÄNEN, MARKO, Protein secretion in *Trichoderma reesei*. Expression, secretion and maturation of cellobiohydrolase I, barley cysteine proteinase and calf chymosin in Rut-C30. - Proteiinien erittyminen *Trichoderma reesei*:n. Sellobiohydraasi I:n, ohran kysteiniiproteiinaasin sekä vasikan kymosiinin ilmeneminen, erittyminen ja kypsyminen Rut-C30-mutanttikannassa. 107 p. (173 p.) Yhteenveto 2 p. 2002.
- 110 TIROLA, MARJA, Phylogenetic analysis of bacterial diversity using ribosomal RNA gene sequences. - Ribosomaalisen RNA-geenin sekvenssien käyttö bakteeridiversiteetin fylogeneettisessä analyysissä. 75 p. (139 p.) Yhteenveto 2 p. 2002.
- 111 HONKAVAARA, JOHANNA, Ultraviolet cues in fruit-frugivore interactions. - Ultravioletin ekologinen merkitys hedelmiä syövien eläinten ja hedelmäkasvien välisissä vuorovaikutussuhteissa. 27 p. (95 p.) Yhteenveto 2 p. 2002.

## JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE

- 112 MARTTILA, ARI, Engineering of charge, biotin-binding and oligomerization of avidin: new tools for avidin-biotin technology. - Avidiinin varauksen, biotiininsitomisen sekä oligomerisaation muokkaus: uusia työkaluja avidiini-biotiiniteknologiaan. 68 p. (130 p.) Yhteenveto 2 p. 2002.
- 113 JOKELA, JARI, Landfill operation and waste management procedures in the reduction of methane and leachate pollutant emissions from municipal solid waste landfills. - Kaatopaikan operoinnin ja jätteen esikäsittelyn vaikutus yhdyskuntajätteen biohajoamiseen ja typpipäästöjen hallintaan. 62 p. (173 p.) Yhteenveto 3 p. 2002.
- 114 RANTALA, MARKUS J., Immunocompetence and sexual selection in insects. - Immunokompetenssi ja seksuaalivalinta hyönteisillä. 23 p. (108 p.) Yhteenveto 1 p. 2002.
- 115 OKSANEN, TUULA, Cost of reproduction and offspring quality in the evolution of reproductive effort. - Lisääntymisen kustannukset ja poikasten laatu lisääntymispanoksen evoluutiossa. 33 p. (95 p.) Yhteenveto 2 p. 2002.
- 116 HEINO, JANI, Spatial variation of benthic macroinvertebrate biodiversity in boreal streams. Biogeographic context and conservation implications. - Pohjaeläinyhteisöjen monimuotoisuuden spatiaalinen vaihtelu pohjoisissa virtavesissä - eliömaantieteellinen yhteys sekä merkitys jokivesien suojelulle. 43 p. (169 p.) Yhteenveto 3 p. 2002.
- 117 SIIRA-PIETIKÄINEN, ANNE, Decomposer community in boreal coniferous forest soil after forest harvesting: mechanisms behind responses. - Pohjoisen havumetsämaan hajottajayhteisö hakkuiden jälkeen: muutokseen johtavat mekanismit. 46 p. (142 p.) Yhteenveto 3 p. 2002.
- 118 KORTET, RAINE, Parasitism, reproduction and sexual selection of roach, *Rutilus rutilus* L. - Loisten ja taudinaiheuttajien merkitys kalan lisääntymisessä ja seksuaalivalinnassa. 37 p. (111 p.) Yhteenveto 2 p. 2003.