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Markus J. Rantala

Immunocompetence and Sexual Selection in Insects

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ABSTRACT

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Males of many species have extravagant morphological and behavioral secondary sexual traits, and female choice of mates is often based on these traits. It has been postulated that such traits are reliable indicators of male quality since the costs of these traits select against cheating. The immunocompetence handicap hypothesis is a recently proposed mechanistic explanation of these costs: it states that males carry sexual ornaments at the expense of their resistance to diseases and parasites, and this resistance is heritable. In this thesis I show that visual, acoustic, and chemical sexual ornaments as well as some behavioral traits in insects may reflect male immunocompetence. Moreover, I show that both immunocompetence and sexual ornaments are condition dependent using experimental manipulations of condition and recording pheromone attractiveness. This provides an explanation for the positive correlation between the expression of sexual ornaments and immunocompetence found at the population level. In addition, I show that in the resource holding polygyny mating system, where females choose territories based on the quality and quantity of resources, the outcome of male-male competition can be used to predict male immunocompetence. A number of studies in insects have proven that immunocompetence is heritable. Thus, by preferring males with elaborate secondary traits or males possessing the best territories females might benefit indirectly by increasing the parasite resistance of their offspring.

Key words: Calopteryx splendens; Calopteryx virgo; courtship song; dominance; Gryllus bimaculatus; immunocompetence; pheromones; sexual selection; sexual signalling; Tenebrio molitor; wing spot.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by Roman numerals I – VI. I have personally written papers I – V and performed most of the work. In paper VI I have performed a significant proportion of the work.

I Rantala, M. J., Koskimäki J., Suhonen, J., Taskinen, J. & Tynkkynen, K. 2000. Immunocompetence, developmental stability and wing spot size in Calopteryx splendens L. Proc. R. Soc. Lond. B 267, 2453-2457

II Rantala, M.J., Jokinen, I., Kortet, R. Vainikka, A. & Suhonen, J. 2002. Do pheromones reveal male immunocompetence? Proc. R. Soc. Lond. B, in press.

III Rantala, M.J., Kortet, R. Kotiaho, J. S., Vainikka, A. & Suhonen, J. 2002 Condition dependence of pheromones and immune function in the grain beetle Tenebrio molitor. Submitted.

IV Rantala, M. J. 2002. Courtship song and immune function in a field cricket. Submitted.

V Rantala, M. J. & Kortet, R. 2002. Male dominance and immunocompetence in a field cricket. Submitted.

VI Koskimäki, J., Rantala, M. J., Taskinen, J., Tynkkynen, K., & Suhonen, J. 2002. Immunocompetence and resource holding potential in the damselfly, Calopteryx virgo L. Behav. Ecol., in revision.

1 SEXUAL SELECTION

Sexual selection is presumed to give rise to extravagant secondary sexual traits and behaviour (Darwin 1871) and a considerable body of experimental and comparative evidence supports this hypothesis (Andersson 1994). Sexual selection arises from the advantages that certain individuals have over other of the same sex and species in relation to reproduction (Darwin 1871). Two processes may lead to sexual selection: competition among individuals of the chosen sex, usually male-male competition, and choice of partners by individuals of the choosy sex, usually females. In many species, females base their choice on the degree of expression of the males' secondary sexual characters (reviewed by Andersson 1994). There are two major theories of sexual selection that are based on female choice of a male sexual character: Fisherian self-reinforcing theory and Handicap theory.

1.1 Fisherian self-reinforcing theory

The Fisherian self-reinforcing theory (Fisher 1930) is based on assumptions that there is heritable variation in male secondary sexual trait size and that female choice is genetically coupled to male trait such that certain female genotypes will preferentially mate with certain male genotype. As both the male trait and female preference for it increase over time, the two processes build on one another, creating a situation often referred to as "runaway selection". The costs of the exaggerated expression of the sexual trait will finally prevent further exaggeration of the trait creating an equilibrium line between costs and benefits and thus putting the runaway process to a rest (Fisher 1930, O'Donald 1980, Lande 1981, Kirkpatrik 1982). Traits that were once attractive because they were well-adapted for survival remain attractive only because they are attractive to females (Pomiankowski & Iwasa 1998).

1.2 Handicap theory

Zahavi (1975) suggested that females prefer males with elaborated sexual displays because they are handicaps and therefore act as a reliable signal of a male's genetic quality. Costly sexual ornaments demonstrate a male's ability to survive in spite of the handicap. If any of this ability is heritable, then the tendency to be good at surviving will be passed on to the offspring. Thus females select for good genes by selecting to mate only with males whose displays honestly indicate their genetic quality. The handicap principle was severely criticised (e.g. Davis & O'Donald 1976, Maynard Smith 1976) because the first simple models suggested that it could not work. However, Zahavi (1977) proposed that if one considers not only the genetic component of male condition but also male phenotypic condition then the handicap principle may work. Afterwards it has been shown that the handicap principle may be modelled successfully especially if condition dependence of a male trait is considered (e.g. Andersson 1982, Pomiankowski 1987, 1988, Heywood 1989, Hoelzer 1989, Grafen 1990a,b, Iwasa et al. 1991, Iwasa & Pomiankoski 1994, Johnstone 1994, Yachi 1995, Kokko 2001).

Hamilton & Zuk (1982) suggested that the resistance to parasites may be one important genetic quality revealed through secondary sexual characters. By choosing a well ornamented male, a female tends to acquire for her offspring those resistance genes which are at the moment important against the predominant parasites. In concordance with the handicap principle (Zahavi 1975, 1977), individuals in good health are able to produce more elaborate sex characters than infected individuals because these signals are costly to produce. Many observational and experimental studies support Hamilton & Zuk's hypothesis (e.g. Møller 1988, 1990, Clayton 1990, Milinski & Bakker 1990, Zuk, et al. 1990a, b, Houde & Torio 1992, Saino & Møller 1996, Taskinen & Kortet 2002, for reviews, see Clayton 1991, Møller & Saino 1994), but no such relationship was found in many other studies (Hamilton & Poulin 1997).

The immunocompetence handicap hypothesis offers a mechanistic extension to Hamilton & Zuk's version of the handicap theory (Folstad & Karter 1992, Wedekind & Folstad 1994). According to the immunocompetence handicap hypothesis, sexual trait expression may be constrained through a trade-off with immune function. The hypothesis suggests that secondary sexual characters develop in response to circulating androgens (or other self-regulating biochemicals that increase the expression of secondary sexual characters but reduces the functioning of the immune system), which on the other hand suppress the ability of individuals to raise an immune defense against parasites (Folstad & Karter 1992). The immunocompetence handicap hypothesis argues that because the production of a secondary sex trait is costly, animals may have to shift energy and metabolites from other tissue to produce well-developed secondary sex characters. Sex hormones may accomplish this by shutting off

energy from the immune system and other systems, so that it can be redirected for production of secondary sex traits (Folstad & Karter 1992). The "good genes" which females might acquire by choosing highly ornamented males might be genes affecting immunocompetence directly or genes having more or less indirect effects on the immune system via body condition, for example, genes affecting the rules by which resources are allocated to the immune system, the cost of ornament expression, or resource acquisition (Westneat & Birkhead 1998).

Male sexual ornaments have often been shown to be strongly condition dependent (e.g. Hill 1992, Gustafsson et al. 1995, Hunt & Simmons 1997, David et al. 1998, David et al. 2000, Kotiaho et al. 2001). Since sexual ornaments are often costly to produce and maintain (e.g. Kotiaho 2001), only individuals in good condition can afford to produce extravagant sexual ornaments and, at the same time, have a sufficient amount of resources left for immune system. This might lead into a positive correlation between male immunocompetence and sexual advertisement. In this thesis I tested whether traits preferred by females are correlated with male immunocompetence in insects.

2 IMMUNOCOMPETENCE AND MEASURES OF IMMUNE DEFENSE IN INSECTS

One widely used definition of immunocompetence is the ability of individual's immune system to resist and control pathogens or parasites (Norris & Evans 2000). In my thesis I have used this definition of immunocompetence.
Insects differ remarkably from vertebtates when it comes to resisting parasitic infections. Whereas vertebrates rely on both adaptive (specific) and innate (unspecific) immunity, insects have only innate immune mechanisms (Hoffman et al. 1999). In insects, one of the most informative ways to assay immunocompetence is to measure the cellular encapsulation response to a novel and standardised antigen such as a nylon monofilament (König & Schmid-Hempel 1995, Rantala et al. 2000, Ryder & Siva-Jothy 2000, Siva-Jothy 2000, Rantala et al. 2002). Encapsulation is a cellular immune response through which insects defend themselves against foreign particles (Salt 1970). During the encapsulation process, specialized haemocytes recognise invading particles as non-self and cause other haemocytes to aggregate and capsulate the particle. A cascade of reactions involving the tyrosine-phenyloxidase pathway causes the melanisation of the capsule and the death of the invading particle (Fisher 1963). Phenoloxidase (PO) is a key enzyme in the synthesis of melanin and the ability to produce melanin is an important aspect of the immune response (Gillespie et al. 1997). Encapsulation response plays also a role in the defence against viruses (Washburn et al. 1996). The humoral system, on the other hand, is comprised of myriad of soluble proteins and enzyme cascades, which play important roles in recognising, signalling and attacking foreign targets (Leonard et al. 1985) and probably in coordinating the cellular responses (Pech & Strand 1995).

3 IMMUNOCOMPETENCE AND SEXUAL SELECTION; RESULTS AND DISCUSSION

3.1 Visual traits: conspicuous colours

Conspicuous colours, feather plumes, enlarged fins, and other visual signals are the most famous secondary sexual characters and the most spectacular of these traits are commonly referred to as ornaments. These traits have shown to attract and stimulate mates and to affect mate choice (e.g. Andersson 1994).

In this thesis I tested whether conspicuous secondary sexual colours preferred by females reflect a male's immune system status (I). As a model species I used Calopteryx splendens Harris. Males of this species have blue wing spots, the size of which exhibits remarkable local and geographical variation (Valle 1937, 1957, Dumondt et al. 1993, Siva-Jothy 1999). It has been found in the subspecies, C. splendens xanthostoma, that females prefer to mate with large spotted males (Siva-Jothy 1999). Previous studies with another damselfly species have revealed that male wing colouration pigments are constituted from melanin (Hooper et al.1999). Melanin is a key component of the humoral immune system, and plays a central part of the encapsulation response (Ratcliffe 1993). I found that the wing spot size was positively correlated with the encapsulation rate, indicating that more ornamented males have a better immunocompetence (I).

3.2 Chemical traits: pheromones

Pheromones are chemical signals that are released by an individual into the environment and which affect the physiology or behaviour of other members of the same species (Beauchamp et al. 1976). They are transmitted through a me-

dium such as air or water by diffusion and may be effective in very small concentrations. Pheromones are one of the most commonly used social signals among organisms (Arnold & Houck 1982, Birch & Haynes 1982). Pheromones function as mate attractors (Eisner & Meinwald 1995), but they may also relay other information to prospective mates. For example, pheromones may signal information about nuptial gifts (Dussourd et al. 1991), developmental stability (Thornhill 1992, Rikowski & Grammer 1999), dominance status (Moore et al. 1997) or male parasite load (Penn & Potts 1998). Pheromones have also been suggested to function in kin recognition (Smith 1983, Simmons 1990).

I investigated whether pheromones transmit information about male immunocompetence and whether pheromones and immunocompetence are dependent on male nutritional condition. My model species, mealworm beetle Tenebrio molitor L. (Coleoptera, Tenebrionidae), is a cosmopolitan pest of stored grains. There is no obvious sexual dimorphism in this species. However, each sex produces distinct pheromones that attract members of the opposite sex (Happ 1969, August 1971, Tanaka et al. 1986). The pheromone of the male has been observed to stimulate the female´s locomotion activity, to promote the aggregation of females in the vicinity of the male and to enhance copulatory behaviour (August 1971, Tanaka et al. 1986, Hurd & Parry 1991).

A previous study with T. molitor showed that infection by a tapeworm, Hymenolepis diminuta, reduces the attractiveness of male pheromones (Worden et al. 2000). This suggests that parasite-mediated sexual selection may occur in this species (Worden et al. 2000). I show that female mealworm beetles, T. molitor, prefer pheromones from males with better immunocompetence, measured as an encapsulation rate against a novel antigen and level of phenoloxidase in the haemolymph (II). In addition, I show that both the attractiveness of male pheromones and immunocompetence are condition dependent both being down-regulated by nutritional stress (III).

3.3 Acoustic traits: courtship song

Acoustic traits are among the most commonly used sexual traits (Andersson 1994). Acoustic signals are good targets of female choice because acoustic signals have shown to be repeatable within males and variable between males (see e.g. Hoikkala & Isoherranen 1997) and they are energetically costly to produce (e.g. Vehrencamp et. al. 1989, Wells & Taigen 1989, Kotiaho et al. 1998).

In this thesis I investigate whether acoustic signals could convey information about male immunocompetence (IV). As a model species I used the Mediterranean field cricket, Gryllus bimaculatus DeGeer. G. bimaculatus, is widely distributed in southern Europe. G. bimaculatus males produce calls that act as signals for mate attraction and the repulsion of rivals (Simmons 1988). Male crickets use modified wings called tegmina to produce three major songs with

aggression, calling, and courtship functions (Alexander 1961). In the laboratory, it has been shown that in male G. bimaculatus size is positively correlated to call intensity and syllable repetition rate (Simmons 1988), but in the field, the syllable rate was negatively related to male size, and the duration of syllables was positively related to size (Simmons & Zuk 1992). Females are sensitive to variation in syllable rate (Doherty 1985, Schidberger 1985) preferring calls with higher rates (Shuvalov & Popov 1973, Simmons 1988a). I made a playback experiment where I played courtship song from two male crickets to a female. I find that G. bimaculatus females, prefer the courtship song of male with better immunocompetence measured as higher encapsulation rate (IV).

3.4 Behavioral traits: dominance status

Females of many species are known to prefer dominant males as mates and in some species females even incite competition between males and then mate with the most dominant male (Berglund et al. 1996). In this thesis I tested whether dominant males had higher immunocompetence than their subordinates in the mediterranean field cricket, G. bimaculatus and whether dominant males are more successful in obtaining matings in situation where both male-male competition and female choice occur (V). Arranging male cricket fighting matches has been a popular pastime in the Orient for nearly a thousand years (Alexander 1961, Hofmann & Stevenson 2000). In this study I used similar types of fighting trials as Chinese gamblers. I found that dominant males had better immunocompetence indicated by higher lytic activity and encapsulation rate than subordinate males of the same size (V). Dominant males were also more successful to obtain matings (V).

3.5 Immunocompetence and resource defence polygyny

In resource defense polygyny mating system, males defend a physical resource, generally a boundaried territory, against other males; females are welcome on the territory as mates of the territory holder. Females choose territories based on the quality and quantity of the resources therein, so males who can defend large, quality territories against challengers stand to gain the most matings (Emlen & Oring 1977).

In this thesis I tested whether a male's resource holding potential is correlated with his immune system status (VI). As a model species I used Calopteryx virgo L. Males of C. virgo defend territories containing one or more oviposition sites for females (e.g. Pajunen 1966, Waage 1973). Territory ownership is settled by aerial contests that can become highly escalated and prolonged between closely matched contestants (Marden & Rollins 1994, see also Fitzstephens &

Getty 2000). Escalated damselfly territorial contests are energetic wars of attrition, which can last even several hours (Marden & Waage 1990). Previous studies have shown that the most important factor affecting the outcomes of the odonates contests are males' fat reserves (Marden & Waage 1990, Plaistow & Siva-Jothy 1996). I staged contests between males and found that winners of the contests showed higher immunocompetence, measured as encapsulation rate when compared to losers (VI). Furthermore, I found that the encapsulation response correlated positively with an individual's fat reserves. I also found that winners in territorial fights had larger fat reserves (VI). Thus, its seems that male resource holding potential and immunocompetence are positively correlated. The positive relationship between male energy reserves and immunocompetence is consistent with the idea that immune function is costly, as recently demonstrated by Moret and Schmid-Hempel (2000) in a study performed on bumblebees (Bombus terrestris). If both immunocompetence and resource holding potential depend on energy reserves, there may be a trade-off between disease resistance and energetically costly territorial behavior. Furthermore, the results suggest that the outcome of a male-male competition (ownership of the territory) can be used by a female to predict male immunocompetence.

CONCLUSIONS

The immunocompetence handicap hypothesis (Folstad & Karter 1992) predicts that the expression of a preferred sexual trait will be positively correlated with pathogen resistance (see also e.g., Ryder & Siva-Jothy 2000). However, empirical studies testing this hypothesis in insects are scarce. In this thesis I have presented empirical evidence that at least some secondary sexual traits of males preferred by females are correlated positively with male immunocompetence at population level. Furthermore I show that both secondary sexual traits and immunocompetence could be condition dependent, which might be an explanation for the positive correlation between the expression of sexual ornaments and immunocompetence often found at the population level. Handicap models of sexual selection suggest that preferences are selected for in females because the preferred characters are correlated with some aspect of male quality from which females can benefit (reviewed in Johnstone 1995). A number of studies have shown that variation in encapsulation ability and haemocyte load can be heritable in insects (e.g. Carton & Boulétreau 1985, Carton et al. 1992, Kraaijeveld & Godfray 1997, Fellowes et al 1998, Kraaijeveld et al. 2001, Ryder & Siva-Jothy 2001) and Kurtz & Sauer (1999) detected heritable variation in lytic activity and phagocytosis ability of an insect. Thus, by preferring males with elaborate secondary traits or males possessing the best territories females could avoid infections and might benefit indirectly by increasing the parasite resistance of their offspring.

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YHTEENVETO

Immunokompetenssi ja seksuaalivalinta hyönteisillä

Useiden eläinlajien koirailla on näyttäviä seksuaaliornamentteja, joiden perusteella naaraat valitsevat pariutumiskumppaninsa. On ajateltu, että nämä ornamentit kuvastaisivat rehellisesti koiraan laatua, sillä ornamenttien tuottamisen kustannus estäisi huonolaatuisten koiraita tuottamasta suurta ornamenttia. Ornamentin tuottamisen kustannukseksi on esitetty ”immuniteettihaitta”-hypoteesi, jonka mukaan ornamenttien tuottaminen heikentäisi yksilön immuniteettikykyä, jolloin vain huippukuntoinen koiras pystyisi tuottamaan suuren ornamentin ja pysymään silti hengissä. Väitöskirjassani tutkin immuniteettikykyä ja sukupuoliornamentteja hyönteisillä. Tutkimuksissani havaitsin että eräät naaraiden suosimat visuaaliset, kemialliset ja akustiset signaalit sekä menestyminen koiraiden välisessä kilpailussa kuvastavat hyvin koiraan immuniteettikykyä. Havaitsin myös, että seksuaaliornamentit sekä immuniteettikyky riippuvat koiraan yleiskunnosta. Tämä saattaa selittää positiivisen korrelaation immuniteettikyvyn ja seksuaaliornamentin välillä. Tutkimuksissani osoitan myös, että pariutumissysteemissä, jossa naaraan valinta ei perustu koiraan laatuun vaan koiraan puolustamaan resurssiin, koiras-koiras -kilpailu johtaa siihen, että naaras saa pariutumiskumppanikseen immunipuolustuskyvyltään parhaan koiraan. Useat aiemmat tutkimukset hyönteisillä ovat osoittaneet yksilön immuniteettikyvyn olevan periytyvää, joten suosimalla koiraita, joilla on puoleensavetävät sukupuolikoristeet, naaraat saavat jälkeläisiä, joilla on hyvä immuniteettikyky.

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ORIGINAL PAPERS

I

Immunocompetence, developmental stability and wing spot size in *Calopteryx splendens* L.

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II

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III

Condition dependence of pheromones and immune function in the grain beetle *Tenebrio molitor*

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IV

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V

Male dominance and immunocompetence in a field cricket

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VI

Immunocompetence and resource holding potential in the damselfly, *Calopteryx virgo* L.

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