









## ABSTRACT

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Interspecific interactions and selection on secondary sexual characters in damselflies

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Diss.

Interspecific interactions related to species recognition can cause selection and affect the evolution of secondary sexual characters. Such interactions include for example avoidance of maladaptive hybridization and interspecific aggression. In this thesis, I focus especially on interspecific aggression and on selection which it may cause on sexual characters of the damselfly, *Calopteryx splendens*. Males of *C. splendens* have pigmented wing spot as a sexual character in the middle of their wings. Large-spotted *C. splendens* males resemble another species *Calopteryx virgo*, males of which have almost completely pigmented wings. I observed character displacement in *C. splendens* males such that the wing spot size decreased with increasing relative abundance of *C. virgo*. Territorial *C. virgo* males reacted more aggressively and from greater distance towards large- than small-spotted *C. splendens* males. This suggests that the character displacement may have evolved because of the interspecific aggression arising from mistaken species recognition. Interspecific aggression causes negative survival selection on wing spot size of *C. splendens* males. In addition, interspecific aggression leads to interspecific territoriality in which large-spotted *C. splendens* males seem to have reduced ability to obtain or keep a territory. Reduced territory holding ability may have negative effects on mating success of large-spotted *C. splendens* males. This is because in contrast to other studies with *Calopteryx* species, in wild sympatric populations females did not mate with large-spotted males. My results clearly show that interspecific aggression is able to cause selection on sexual characters and thus has potential to affect the evolution of secondary sexual characters.

Key words: Calopterygidae; character displacement; interspecific aggression; interspecific territoriality; male mating success; reinforcement; sexual selection; survival; sympatry.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following four papers, which will be referred to in the text by their Roman numerals I - IV. I have written all of the papers. In addition, I have performed a large part of the field work and a major part of the analyses in each paper.

- I Tynkkynen, K., Rantala, M. J. & Suhonen, J. 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *Journal of Evolutionary Biology* 17: 759–767.
- II Tynkkynen, K., Kotiaho, J. S., Luojumäki, M. & Suhonen, J. Interspecific territoriality between *Calopteryx splendens* and *Calopteryx virgo* damselflies: the role of secondary sexual characters. Submitted.
- III Tynkkynen, K., Kotiaho, J. S., Luojumäki, M. & Suhonen, J. Interspecific aggression causes negative selection on sexual characters. Submitted.
- IV Tynkkynen, K., Kotiaho, J. S., Luojumäki, M. & Suhonen, J. Selection analyses on male mating success in wild sympatric populations of damselflies *Calopteryx splendens* and *Calopteryx virgo*. Manuscript.



# 1 INTRODUCTION

Secondary sexual characters are conventionally considered to evolve as a result of selection operating within the species through female choice (Andersson 1982, 1994; Kirkpatrick & Ryan 1991; Kokko et al. 2002) or male-male competition (Arak 1983; Andersson 1994). It has also been recognized that interspecific interactions may cause selection on sexual characters. These kinds of interactions include at least avoidance of maladaptive hybridization (Dobzhansky 1951; Waage 1975, 1979; Sætre et al. 1997; Marshall & Cooley 2000; Höbel & Gerhardt 2003; Lemmon et al. 2004), predation (Endler 1980; Zuk et al. 1998; Stoddard 1999) and interspecific aggression (Butcher & Rohwer 1989, Sætre et al. 1993; Alatalo et al. 1994; Tynkkynen et al. 2004), although the last has been almost entirely neglected in empirical investigations. In this thesis, I concentrate especially on interspecific aggression and its potential to cause selection on secondary sexual characters.

## 1.1 Interspecific interactions and the definition of character displacement

Probably the most studied interspecific interaction in the face of secondary sexual characters is the avoidance of maladaptive hybridization. When two species hybridize or mate with each other such that the fitness of the parents is reduced, selection to avoid interspecific mating may arise. As a consequence, mate preferences or sexual characters of the two species may diverge. The process is referred to as 'reinforcement' because it should reinforce premating reproductive isolation of the species (e.g. Howard 1993; Noor 1995, 1999; Márquez & Bosch 1997; Sætre et al. 1997; Rundle & Schluter 1998; Higgie et al. 2000; Marshall & Cooley 2000; Gabor & Ryan 2001; Höbel & Gerhardt 2003; Lemmon et al. 2004). The resulting divergence in mate preference or sexual characters between sympatric and allopatric populations is known as 'reproductive character displacement' (e.g. Howard 1993; Lemmon et al. 2004).

Butlin (1987; 1989) defines the terms slightly differently. He suggests that the term reinforcement should only be used when the process is occurring between two incipient species, which are able to produce only partially viable or fertile offspring. In such a case, reinforcement should be a process which has a role in completing the process of speciation (see also Liou & Price 1994; Noor 1999). According to Butlin (1987; 1989), reproductive character displacement also describes the process, which strengthens reproductive isolation, but the use of the term should be restricted to cases where the speciation of two species is already complete, i.e. when mating between heterospecifics does not lead to production of viable or fertile offspring. However, Butlin's definition has been criticized (e.g. Lemmon et al. 2004), and throughout the thesis I use Howard's (1993) definition of the terms. Howard (1993) emphasizes reinforcement as a process, which strengthens preexisting reproductive isolation and reproductive character displacement as a pattern which can result from reinforcement (Howard 1993).

Reproductive character displacement is not always caused by reinforcement, however. For example, similar patterns may arise from interference in mate recognition signals of species that do not hybridize (see Howard 1993; Noor 1999) or because of interspecific aggression (Alatalo et al. 1994). I suggest that in such cases the term reproductive character displacement should not be used. Hereafter, I restrict the use of the term in the cases where the pattern is caused by avoidance of maladaptive hybridization; in other cases I refer simply to 'character displacement'. In addition, although character displacement is traditionally measured by comparing characters between allopatric and sympatric populations (e.g. Grant 1994; Schluter 2000), it can also be measured by using relative abundances or proportions of species in sympatric populations (Saloniemi 1993; Pfennig & Murphy 2002; Tynkkynen et al. 2004; see also Howard 1993; Noor 1995).

## 1.2 Interspecific aggression

Selection on divergence of sexual characters of species can arise as a consequence of interspecific aggression. Interspecific aggression is usually interpreted to result from interspecific interference competition over resources (Murray 1981; Nishikawa 1987; Marvin 1998; Genner et al. 1999), although it may also originate from mistaken species recognition. In the latter case, aggressive behaviour related to territorial defence can mistakenly be directed towards heterospecific individuals due to their phenotypic similarity (Murray 1971, 1981, 1988; Nishikawa 1987; Alatalo et al. 1994).

Interspecific aggression arising either from mistaken species recognition or from interference competition over resources may be able to cause selection on male sexual characters. Species can be phenotypically similar in their secondary sexual characters, which may lead to misdirected aggression towards

heterospecific individuals. In both cases, interspecific aggression can reduce the fitness of the victims. For example, interspecific aggression may force individuals of subdominant species to less preferred habitats or territories (Alatalo et al. 1994; Nomakuchi & Higashi 1996; Martin & Martin 2001), it may reduce attractiveness of males to females when males are targets of excessive interspecific harassment or it may reduce the survival of individuals through injuries or depletion of energy reserves. Thus, interspecific aggression may also be able to cause character displacement on sexual characters.

### 1.3 Aims of the study

In this thesis, I studied interspecific interactions and phenotypic selection on secondary sexual characters caused by these interactions. I focused especially on interspecific aggression and on its consequences. Study organisms were two damselfly species, *Calopteryx splendens* and *C. virgo*, the former of which has pigmented wing spots as secondary sexual characters. In paper I, I investigated the variation in wing spot size of *C. splendens* males, and whether the variation exhibit a pattern of character displacement. In addition, I investigated interspecific aggression and territory holding ability between the two species to determine possible cause for character displacement. In papers II-IV I studied more closely the mechanisms through which interspecific aggression may cause selection on wing spot size of *C. splendens* males. In paper II I concentrated on the occurrence of interspecific territoriality between the two species and determined how the presence of *C. virgo* males affects the territoriality and time allocation of *C. splendens* males. In paper III I studied survival selection on wing spot size of *C. splendens* males in relation to the relative abundance of *C. virgo* males, and in paper IV I focused on male mating success.

## 2 STUDY SPECIES

The banded demoiselle *Calopteryx splendens* Harr. and the beautiful demoiselle *C. virgo* L. are two closely related damselfly species (Odonata: Calopterygidae) which resemble each other both ecologically and phenotypically. There are slight differences in the habitat requirements of the species in the adult (Askew 1988) and larval stage (Schütte & Schrimpf 2002), but both species inhabit streams with patches of aquatic vegetation (Askew 1988). In Finland, the two species are sympatric across the range of *C. splendens*, but allopatric *C. virgo* populations are common (Karjalainen 2002). Hybrids between the two species occur in nature [hybrids revealed by RAPD-technique; Tynkkynen, K., Grapputo, A., Kotiaho, J. S., Rantala, M. J. Väänänen, S. & Suhonen, J., unpublished data; see also De Marchi (1993) and Corbet (1999)].

Males of *C. splendens* and *C. virgo* both have dark pigmentation with blue reflection in their wings as secondary sexual characters. Wings of *C. virgo* are almost completely pigmented, but *C. splendens* have pigmented wing spots in the middle of their wings. The wing spot size of *C. splendens* varies within and between populations (Dumont et al. 1993; Rantala et al. 2000; Tynkkynen et al. 2004; Svensson et al. 2004). The reason for the variation has remained unclear, although mechanisms such as climatic factors (Valle 1937) and introgression with closely related species (Dumont et al. 1993) have been suggested. Large wing spots may indicate male quality for females, since larger wing spots are more symmetrical and have less unpigmented areas than smaller wings spots (Rantala et al. 2000) and large-spotted *C. splendens* males have better immunocompetence than small-spotted males (Rantala et al. 2000; see also Siva-Jothy 2000). In addition, in nature large-spotted males may have better survival than small-spotted males as has been found in other calopterygid damselflies (Grether 1996a; Córdoba-Aguilar 2002).

Males of both species defend floating river vegetation as territories (Pajunen 1966; Gibbons & Pain 1992). Females use these vegetation patches as oviposition sites (Pajunen 1966; Gibbons & Pain 1992; Siva-Jothy et al. 1995), and they usually mate with the territory holder (see Siva-Jothy et al. 1995; Plaistow & Siva-Jothy 1996). Males court females by displaying courtship flight

in which they introduce their wing pigmentation to females (e.g. Pajunen 1966; Askew 1988; Siva-Jothy 1999). Non-territorial males exist, but they have substantially lower reproductive success than territorial males (Plaistow & Siva-Jothy 1996). In closely related *Calopteryx* species, females base their mate choice on the quality of male territory (Gibbons & Pain 1992; Siva-Jothy et al. 1995) and when territory quality is taken into account, on wing pigmentation of males (Siva-Jothy 1999; Córdoba-Aguilar 2002). Females get direct benefit for their mate choice: egg survival and hatching success is higher in territories where river flow rate is appropriate (Siva-Jothy et al. 1995). Females may also prefer mates which do not suffer excessive attacks from other males (Hooper & Siva-Jothy 1997).

### 3 RESULTS AND DISCUSSION

#### 3.1 Interspecific aggression and character displacement (I)

To observe possible character displacement in wing spot size of *C. splendens* males, I collected correlational data from 25 populations on the relationship between wing spot size and relative abundance of *C. virgo* males. To calculate the relative abundance of *C. virgo* males, I divided the total number of *C. virgo* males by the total number of both species. In six populations, I also investigated interspecific aggression experimentally by observing aggression of *C. virgo* males towards large- and small-spotted *C. splendens* males. In addition, in three populations I determined the territory holding ability of males in interspecific contests.

I observed character displacement in *C. splendens* males such that wing spot size decreased with increasing relative abundance of *C. virgo* males. There was no comparable pattern in wing length. Furthermore, *C. virgo* males reacted more aggressively and from a greater distance towards large- than small-spotted *C. splendens* males, which suggests that interspecific aggression is at least partially based on mistaken species recognition. If interspecific aggression arises from interspecific interference competition over resources, *C. virgo* males should react equally aggressively towards large- and small-spotted *C. splendens* males. In interspecific contest, *C. virgo* males also had better territory holding ability than *C. splendens* males.

Interspecific aggression may cause selection on wing spot size of *C. splendens* males in several ways. First, interspecific aggression may reduce the survival of large-spotted males. This is because fighting is energetically costly (Plaistow & Siva-Jothy 1996) and may lead to injuries. Second, large-spotted *C. splendens* may be unable to obtain or keep a territory or they may be able to obtain only low quality territory because of harassment from *C. virgo* males. Since fighting depletes fat reserves (Plaistow & Siva-Jothy 1996; see also Marden & Waage 1990; Marden & Rollins 1994; Koskimäki et al. 2004), interspecific aggression may also reduce territory holding potential of large-

spotted males. Because territoriality is essential for high lifetime reproductive success (Plaistow & Siva-Jothy 1996), differential interspecific aggression may have a negative effect on fitness of large-spotted *C. splendens* males. Third, interspecific aggression may reduce the attractiveness of large-spotted males to females if aggression increases the time males spend on fighting. In *C. splendens xanthostoma*, females avoid matings with males that suffer from excessive attacks of other males (Hooper & Siva-Jothy 1997).

Provided that wing spot size has additive genetic variation, the pattern of character displacement in wing spot size of *C. splendens* males can be explained by the negative effects of interspecific aggression on large-spotted *C. splendens* males. This is because the higher the relative abundance of *C. virgo* males, the greater is the probability of *C. splendens* males to encounter heterospecifics and the greater the negative effect of interspecific aggression on *C. splendens* males. Alternatively, the pattern may have arisen because of avoidance of maladaptive hybridization; hybrids do occur in nature (Tynkkynen, K., Grapputo, A., Kotiaho, J. S., Rantala, M. J. & Suhonen, J. unpublished data; see also De Marchi 1990; Corbet 1999). However, in species in which females mate multiply, as females of some *Calopteryx* species are able to do (e.g. Siva-Jothy & Hooper 1995, 1996; Cordero & Andrés 2002; Córdoba-Aguilar et al. 2003), the effect of reinforcement may be reduced since the cost of mating with heterospecifics may be reduced (Marshall et al. 2002; see also Veen 2001). In addition, if interspecific aggression is able to cause divergence on sexual characters, species recognition should be facilitated thus reducing occurrence of hybridization.

### 3.2 Interspecific territoriality (II)

The aim of this study was to determine how the presence of *C. virgo* males affects the territoriality and time allocation of *C. splendens* males. In addition, I observed the effect of wing spot size of *C. splendens* males to interspecific territoriality. To do this, I performed a three-day experiment in which I removed *C. virgo* males from seven wild populations and compared behavioural data gathered before and after the removal.

After the removal of *C. virgo* males, the number of territorial *C. virgo* males increased. This indicates that there exists interspecific territoriality between the two species. Interspecific territoriality was also influenced by the wing spot size of *C. splendens* males. This is because before the removal of *C. virgo* males, wing spot size of territorial and non-territorial males did not differ. This is in contrast to other studies conducted with other calopterygid damselflies, in which territorial males have larger wing spots or higher proportion of wing pigmentation than non-territorial males (Grether 1996b; Siva-Jothy 1999; Córdoba-Aguilar 2002). However, this pattern did not change after the removal of *C. virgo* males. This may be because after the removal, I only allowed one day for males to adjust their territorial status. This may have been too short of a

time period because after the removal of *C. virgo* males the time *C. splendens* males spent in intraspecific contests increased indicating that males were still fighting over vacant territories.

Wing spot size of *C. splendens* males also affects interspecific territoriality in other ways. Before the removal of *C. virgo* males there was a positive correlation between the distance of *C. splendens* males to the nearest *C. virgo* territory and wing spot size of *C. splendens* males. This suggests that differential aggression towards *C. splendens* males (I; Tynkkynen et al. 2004) prevents large-spotted *C. splendens* males to obtain territories near *C. virgo* males. Thus, if both species have similar requirements for high quality territories, interspecific aggression between the species forces large-spotted *C. splendens* males onto low quality territories. An alternative explanation is that requirement for territory quality differ between the species and small-spotted *C. splendens* are near *C. virgo* males because of their low resource holding potential in intraspecific contests (see Grether 1996b; Siva-Jothy 1999; Cordoba-Aguilar 2002). However, this is not likely because after the removal of *C. virgo*, large-spotted *C. splendens* males were no longer further away from old *C. virgo* territories. As a consequence, it must have been the interspecific territoriality which inhibited large-spotted *C. splendens* males to obtain a territory near territorial *C. virgo* males.

In contrast to my hypothesis, there was no relationship between wing spot size of *C. splendens* males and time used on interspecific contests before the removal of *C. virgo* males. This result may arise simply because small-spotted *C. splendens* males had their territories nearer to *C. virgo*, and territorial contests may more often take place among the closest neighbours. However, the time that *C. splendens* males used in interspecific contests increased with increasing relative abundance of *C. virgo* males, indicating that the possible negative effects of interspecific aggression are depended on the relative abundance of heterospecific males.

Previously, interspecific territoriality has often been interpreted to originate from interspecific interference competition over resources (e.g. Reed 1982; Catchpole & Leisler 1988; Robinson & Terbourgh 1995; Genner et al. 1999), and the possibility that interspecific territoriality may arise because of mistaken species recognition has attracted little attention (Murray 1971, 1981, 1988; Nishikawa 1987; Alatalo et al. 1994). However, my study reveals that the possibility of mistaken species recognition should not be neglected. More importantly, interspecific territoriality may have evolutionary consequences on sexual characters if males with the most exaggerated sexual characters are not able to obtain or keep a territory or they are forced on low quality territories.



### 3.3 Survival selection on wing spot size of *C. splendens* males (III)

To examine the role of interspecific aggression in causing survival selection on wing spot size of *C. splendens* males, I performed a removal experiment. In the experiment, I manipulated the relative abundance of *C. virgo* males by removing all *C. virgo* males once a week from three treatment populations. In addition, I monitored survival of males in four unmanipulated control populations. I investigated directional selection on survival by means of standardized selection differentials (Endler 1986).

Removal of *C. virgo* males had an effect on the survival selection for wing spot size of *C. splendens* males, but not for wing length. The difference in the strength of the selection on wing spot size between control and treatment populations seemed to be highest when relative abundance of *C. virgo* was high. This is an expected consequence of the removal of *C. virgo* males if survival selection is affected by interspecific aggression. This is because experimental manipulation caused a greater reduction in relative abundance of *C. virgo*, and thus interspecific aggression, when the natural relative abundance of *C. virgo* in the population was high. In addition, directional selection on wing spot size was positive in control populations where relative abundance of *C. virgo* males was low. However, the selective advantage of the large-spotted males decreased with increasing relative abundance of *C. virgo* males. Finally, when the relative abundance of *C. virgo* males was high, there was negative survival selection on wing spot size of *C. splendens*.

Reduced survival of large spotted *C. splendens* males is likely to be a consequence of reduced fat reserves. This is because physical contacts occur rarely in fights of males (Tynkkynen, K. personal observation; see also Pajunen 1966), and because fighting is energetically costly (Plaistow & Siva-Jothy 1996). The time spent in interspecific contests increases with relative abundance of *C. virgo* males (II), suggesting that fat reserves of large-spotted *C. splendens* males are depleted faster as a consequence of interspecific aggression when relative abundance of *C. virgo* males is high. This should have great implications on male lifetime mating success, since territory holding potential of males is dependent on male fat reserves (Marden & Waage 1990; Marden & Rollins 1994; Plaistow & Siva-Jothy 1996; Koskimäki et al. 2004), and territorial males have substantially higher reproductive success than non-territorial males (Plaistow & Siva-Jothy 1996). Since in damselflies longevity is one determinant of male lifetime reproductive success (Banks & Thompson 1985; Forsyth & Montgomerie 1987; Fincke 1988; Cordero 1995), reduced survival may also have a direct effect on male fitness.

### 3.4 Mating success of *C. splendens* males in sympatric populations (IV)

If interspecific aggression or avoidance of maladaptive hybridization has an effect on mating success of *C. splendens* males, the effect should increase with increasing relative abundance of *C. virgo*. This is expected because when relative abundance of heterospecifics increases, the negative effects of the interspecific interactions are also expected to increase. In addition, I studied whether there exists mating selection on wing spot size as has been found in previous studies (Siva-Jothy 1999; Córdoba-Aguilar 2002). To investigate these questions, I monitored male mating success in seven sympatric populations. I estimated directional selection on male mating success by using standardized selection differentials (Endler 1986) and standardized selection gradients (Hardy and Field 1998; Janzen & Stern 1998).

There was no correlation between relative abundance of *C. virgo* males and standardized selection differentials or gradients for wing spot size of *C. splendens* males. I did not detect consistent mating bias towards large-spotted *C. splendens* males in any of the study populations. In closely related *Calopteryx* species females prefer large-spotted males or males with higher proportion of wing pigmentation (Siva-Jothy 1999; Córdoba-Aguilar 2002). My results may arise when female mate choice is influenced by interspecific aggression, avoidance of maladaptive hybridization, or both.

Interspecific aggression may have an effect on female mate choice if the aggression affects the territoriality of *C. splendens* males. My previous study (II) indicates that this seems to be the case: in contrast to other studies with calopterygid damselflies (Grether 1996b; Siva-Jothy 1999; Córdoba-Aguilar 2002), territorial males did not have larger wing spots than other males. Attractiveness of large-spotted *C. splendens* males to females may also be further reduced because of harassment from heterospecific males. Through these mechanisms, it may be that only a small number of *C. virgo* males interfering territoriality of large-spotted *C. splendens* males is necessary to alter the relative reproductive success of large- and small-spotted males.

Reinforcement may also have shaped female mate preference such that females do not prefer large-spotted *C. splendens* males in sympatric populations. However, I did not find reproductive character displacement in female mate choice supporting this hypothesis. This does not exclude the possibility that reinforcement has operated in study populations. This is because reinforcement may exist without apparent reproductive character displacement in female mate preference (Lemmon et al. 2004), and it may be that the pattern is observable only when allopatric and sympatric populations are compared (see Marshall & Cooley 2000). In addition, I did not test reproductive character displacement experimentally, as has been done in other studies (e.g. Noor 1995; Márquez & Bosch 1997; Sætre et al. 1997; Rundle & Schluter 1998; Higgie et al. 2000; Marshall & Cooley 2000; Gabor & Ryan 2001; Höbel & Gerhardt 2003),

and it may be that the pattern is not detectable if only correlational data is used. Furthermore, gene flow (see Sanderson 1989; Servedio & Kirkpatrick 1997) or instability of relative abundance within population may have obscured build-up of reproductive character displacement in the sympatric populations. It may also be possible that interspecific aggression and reinforcement both affect female mate choice in *C. splendens*.

## 4 CONCLUSIONS

Interspecific interactions have been suggested to exert selection and cause variation in secondary sexual characters. Previous studies have mostly concentrated on avoidance of maladaptive hybridization (e.g. Waage 1975; 1979; Sætre et al. 1997), and the role of interspecific aggression has been neglected almost completely (Butcher & Rohwer 1989; Sætre et al. 1993; Alatalo et al. 1994; Tynkkynen et al. 2004). In this thesis, however, I provide evidence that interspecific aggression is able to cause selection on male secondary sexual characters, i.e. wing spot size, in the damselfly *Calopteryx splendens*. My results also suggest that this selection may have had evolutionary consequences on male sexual characters of the species. This is because there was character displacement in *C. splendens* males such that wing spot size decreased with increasing relative abundance of *C. virgo* males.

My findings may aid the future development of the theory of sexual selection, if the fact that interspecific aggression has real potential to cause variation on sexual characters is given more consideration. In addition, as reinforcement (e.g. Noor 1995, 1999; Sætre et al. 1997; Higgie et al. 2000), interspecific aggression may have the potential to reinforce premating reproductive isolation of species. This is because species recognition is likely to be facilitated if the phenotypic similarity of the species decreases as a result of interspecific aggression, thus reducing the occurrence of hybridization. Provided this is the case, interspecific aggression may play a part in completing the speciation process when hybrids occur in nature, much in the same manner that reinforcement might do (e.g. Liou & Price 1994; Noor 1999).

In summary, my results suggest that interspecific aggression should be considered when future studies on variation in secondary sexual characters and reproductive isolation of species are planned. Particular attention should be paid when studying territorial animals in which aggressive interactions are likely to occur.

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## YHTEENVETO

### Lajienväliset vuorovaikutukset ja seksuaaliominaisuuksiin kohdistuva valinta sudenkorenoilla

Lajienväliset vuorovaikutukset voivat aiheuttaa valintaa koiraiden sekundaarisiin seksuaaliominaisuuksiin. Näin on etenkin silloin, kun lajienväliset vuorovaikutukset ovat seurausta lajintunnistusvirheestä, joka perustuu kahden lajin seksuaaliominaisuuksien samankaltaisuudelle. Tällaisia lajienvälisiä vuorovaikutuksia ovat kelpoisuutta heikentävän risteytymisen välttäminen ja aggressiivisuus, mutta etenkin lajienvälisen aggressiivisuuden vaikutusta seksuaaliominaisuuksiin on tutkittu hyvin vähän.

Väitöskirjassani tutkin lajienvälisiä vuorovaikutuksia kahdella lähisukuisella sudenkorentolajilla, immenkorennolla (*Calopteryx splendens*) ja neidonkorennolla (*C. virgo*). Tutkimuksessani keskityin etenkin lajienväliseen aggressiivisuuteen sekä siihen, millaista valintaa lajienväliset vuorovaikutukset voivat saada aikaan immenkorentokoiraiden seksuaaliominaisuuksiin. Immenkorenon sukukypsillä koirilla on seksuaaliominaisuuksina tummansiniset siipivyöt läpikuultavien siipien keskellä. Immenkorentokoiraista poiketen neidonkorentokoiraiden siivet ovat lähes kokonaan tummansiniset. Mitä leveämpi immenkorentokoiraan siipivyö on, sitä enemmän immenkorentokoiras muistuttaa neidonkorentokoirasta.

Tutkimustulosteni mukaan immenkorentokoiraiden siipivyön leveys populaatioissa pieneni neidonkorentokoiraiden suhteellisen osuuden kasvaessa. Tämän ominaisuuden siirtymän perusteella vaikuttaa siltä, että lajienvälisillä vuorovaikutuksilla saattaa olla vaikutusta immenkorentokoiraiden siipivyön leveyteen. Yksi selitys ominaisuuden siirtymään voisi olla lajintunnistusvirheestä syntyvä lajienvälinen aggressiivisuus. Näin siksi, että neidonkorentokoiraat reagoivat pidemmältä etäisyydeltä ja aggressiivisemmin leveä- kuin kapeavöisiin immenkorentokoiraisiin. Jos lajienvälinen aggressiivisuus olisi puhtaasti seurausta resurssikilpailusta, neidonkorentokoiraat reagoisivat yhtä aggressiivisesti leveä- ja kapeavöisiin immenkorentokoiraisiin.

Immenkorentokoiraiden siipivyössä oleva ominaisuuden siirtymä saattaa olla seurausta lajienvälisestä aggressiivisuudesta, mikäli se aiheuttaa negatiivista valintaa siipivyön leveyteen ja mikäli siipivyön leveys on periytyvä ominaisuus. Tutkimustulosteni valossa lajienvälinen aggressiivisuus aiheuttaa valintaa immenkorentokoiraiden siipivyön leveyteen. Ensinnä, lajien välillä esiintyy reviiirillisyyttä siten, että leveävöisten immenkorentokoiraiden kyky hankkia tai säilyttää reviiiri näyttäisi olevan heikentynyt sympatrisissa populaatioissa. Näin siksi, että reviiirittömien ja reviiirillisten koiraiden siipivyön leveyksissä ei ollut eroa. Tämä tulos poikkeaa muilla saman heimon sudenkorenoilla toteutettujen tutkimusten tuloksista, sillä niissä reviiirillisillä koirilla on havaittu olevan leveämmät siipivyöt kuin reviiirittömillä koirilla. Lisäksi, mitä suurempi oli immenkorentokoiraan siipivyö, sitä kauempana sen

reviiri oli neidonkorentokoiraan reviiristä. Neidonkorentojen poiston jälkeen siipivyyden leveydellä ei kuitenkaan ollut vastaavanlaista yhteyttä vanhaan neidonkorentoreviiriin. Tutkimuksessa havaitsin myös, että mitä enemmän populaatioissa oli neidonkorentoja, sitä enemmän immenkorentokoiraat käyttivät aikaa lajien väliseen taisteluun.

Toiseksi, lajienvälinen aggressiivisuus heikentää leveävöisten immenkorentokoiraiden hengissäsäilymistä. Mitä enemmän populaatioissa oli neidonkorentoja suhteessa immenkorentoihin, sitä heikommin leveävöiset immenkorentokoiraat säilyivät hengissä. Vastaavanlaista hengissäsäilyvyyden heikkenemistä neidonkorentojen suhteellisen osuuden kasvaessa ei ollut havaittavissa populaatioissa, joissa neidonkorentokoiraiden määrää oli kokeellisesti pienennetty. Myös tämä tulos tukee käsitystä siitä, että lajienvälinen aggressiivisuus aiheuttaa negatiivista valintaa siipivyyden leveyteen.

Kolmanneksi, lajienvälisellä aggressiivisuudella saattaa olla vaikutusta koiraiden lisääntymismenestykseen. Näin siksi, että toisin kuin muilla saman suvun lajeilla tehdyissä tutkimuksissa, yhdessäkään tutkimuspopulaatioissa naaraat eivät paritelleet leveävöisimpien koiraiden kanssa. Tämä voi olla seurausta leveävöisten immenkorentokoiraiden heikentyneestä kyvystä hankkia tai säilyttää reviiri. Vaihtoehtoinen selitys on, että naaraat eivät parittele leveävöisten koiraiden kanssa välttääkseen lajienvälistä risteytymistä. Näiden syiden erottaminen toisistaan vaatii kuitenkin lisätutkimuksia.

Tutkimustulokseni tuovat uusia ulottuvuuksia seksuaalivalinnan teoriaan, sillä lajienvälinen aggressiivisuus voi selittää joissakin seksuaaliominaisuuksissa esiintyvää vaihtelua. Lajienvälisellä aggressiivisuudella saattaa myös olla vaikutusta kahden lajin lisääntymisisolaatioon. Näin siksi, että jos kahden lajin seksuaaliset ominaisuudet eriytyvät sympatrisissa populaatioissa lajienvälisen aggressiivisuuden seurauksena, myös samaan lajiin kuuluvien pariutumiskumppanien tunnistaminen saattaa helpottua. Lajienvälinen aggressiivisuus voisi siten olla yksi mekanismi, joka voimistaa lajienvälistä lisääntymisisolaatiota.

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