A POINT OF VIEW

FEMALE CHOICE, SECONDARY EFFECT OF « MATE CHECK »? A HYPOTHESIS

RUDY JOCQUÉ

Royal Africa Museum, B-3080 Tervuren, Belgium

e-mail: jocque@africamuseum.be

Abstract. A new hypothesis is formulated to explain the diversity and the range of complexity of secondary sexual characters (SSC). It is based on the observation that in many animal groups an important somatic radiation took place but the SSC remained fairly uniform and their complexity low, while in some other well-studied groups it can be shown that, apparently at a later stage, complexity increased dramatically while somatic morphology remained stable. SSC are therefore hypothesised to be linked to hidden (behavioural), but crucial traits that have been acquired in the last steps of the evolution of the taxon. The mating process is postulated to guarantee the presence of these characters. During this process the « mate is checked ». The reason for this mechanism is hypothesised to be the avoidance of the loss of crucial behavioural adaptations through deleterious mutations. The hypothesis might explain why taxa with a flexible checking system (e.g. stridulation, nuptial dance) are more speciose than those using only morphological clues which may be more limited in complexity and variation. Systems that allow larger variation without compromising the survival of the adult male will allow a wider radiation. Since complexity of SSC is hypothesised to be correlated with specialisation, animal groups with smaller species can be expected to have more complex SSC. Female choice is presumed to be a secondary effect of the « mate check » mechanism. The former only operates in optimal habitats where a wide range of the signal strength of the male is to be expected. In marginal habitats (sinks) it is likely to be insignificant because both female coyness and range of male signal strength are assumed to drop. It is precisely in sinks where speciation will occur when behavioural adaptations, consolidated by SSC, allow more efficient use of underexploited resources. Therefore, in contrast to female choice, mate check is viewed as a stabilising mechanism.

Key words: Araneae, cichlids, complexity, marginal habitats, niche pressure, secondary sexual characters, sexual selection, sinks, sources, specialisation, speciation.

INTRODUCTION

The purpose of sex is currently considered to be an insurance for rapid adaptation under changing environmental conditions. It would appear, however, that this apparently well-established theory might have to be abandoned or at least modified, in the light of new insights (OTTO & MICHALAKIS 1998, and references therein). ZEYL & BELL (1997) provide convincing data which indicate that the real advantage of sex is the elimination of deleterious mutations. Some of the hypotheses concerning sexual selection, in particular Fisherian selection, have also acquired the theory status. Since they are probably less well established

than the former, there is reason to consider that status as premature. The alternative mechanism here presented protracts the direction taken by the hypothesis of ZEYL & BELL (1997).

Sexual selection was for the first time formulated by DARWIN (1859, 1871) and was recognised as one of the driving evolutionary forces. Sexual selection has many aspects: sperm competition, endurance rivalry (lek behaviour) and coercion, but male contests and mate choice are doubtless the mechanisms that have received most attention as they are supposed to be the most widespread mechanisms in this respect (ANDERSSON & IWASA, 1996). We will focus on the latter in the present paper.

As far as mate choice is concerned, a remarkable and well known hypothesis is that of FISHER (1930) known as the «runaway process». According to that model sexual dimorphism is a result of sexual selection *per se*: females choose males for the sake of their ability to stimulate the female which results in a self-reinforcing process, permanently increasing the extent of the secondary sexual characters (SSC: since the terms «primary» and «secondary» sexual characters have led to confusion in the past – see ARNQVIST1997 – SSC is here used as any character, apart from the gonads, that contributes to sexual dimorphism). The reasoning behind this hypothesis is that the female's preference for a certain type of male is heritable and will be similar in her daughters. Fisherian selection is still often invoked to explain sexual dimorphism. Another model that is rapidly gaining influence is the «good genes» hypothesis (also called «handicap» or «indicator» model) which assumes a link between the quality of the male ornament and his overall physical fitness. In other words, the stronger the male's signal, the higher its fitness. This hypothesis was also proposed by FISHER (1930), reformulated by ZAHAVI (1975, 1987) and translated into a population genetic model by GRAFEN (1990). Females selecting a strong male signal would thus be guaranteed higher survival rates of their offspring. A third model that receives increasing attention is a modification of the indicator model called the «revealing indicator model» which expects a certain quality of the male (e.g. resistance against parasites) to be reflected in the male's ornament (HEYWOOD, 1989). A further model is the «direct benefit» hypothesis (KIRKPATRICK 1985, 1987) which assumes that females tend to mate with males that maximize female fecundity. Species recognition is yet another explanation for mate choice and one of the earliest hypotheses to explain it: SSC are assumed to have evolved in order to avoid interspecific mating. Finally, the «sensory exploitation» model (RYAN 1990, RYAN *et al.* 1990, RYAN & KEDDY-HECTOR 1992) assumes that males take advantage of the female sensory capabilities that antedate the origin of the sexual selection dynamic and the evolution of the male and female traits is thus decoupled. It is evident that some of these mechanisms overlap and have been combined to explain particular cases of female choice.

The present paper formulates a new hypothesis that focuses on the quantity of information that is transferred from the male to the female during the entire mating process and is assumed to be a mechanism to avoid deleterious mutations which might easily affect fine-tuned behavioural adaptations.

THE HYPOTHESIS

The nucleus of the hypothesis is as follows :

In order to avoid the loss of crucial behavioural adaptations by deleterious mutations that would compromise survival, incipient species develop secondary sexual characters linked to these adaptations; the mating process is thus construed so that it guarantees the presence of these characters, and during this process the « mate is checked ». This implies that SSC transfer a certain amount of information related to the species' degree of specialisation and that there is no necessity for a causal relationship between the behavioural or somatic trait and the SSC that is linked to it. It has the important implication that female choice is a result of the presence of SSC and not the cause of their origin; whereas female choice is considered to increase the rate of evolution, mate check on the contrary is proposed to have a stabilising effect.

The background to the idea is the fact that parts of the genome are more susceptible to mutations than others. As mutations are more likely to occur in such an active zone, the chance for occurrence of exactly the deleterious mutations that compromise newly acquired adaptations is high . « Mate check » can be considered a mechanism to prevent mates with such deleterious mutations taking part in the reproductive process.

Although the present paper does not intend to formulate a genetic background of the mechanism, one of the possibilities is the implication of pleiotropy. The information that is transferred to the female by morphological or behavioural sexual traits, operating during courtship and mating, has to be genetically linked to the hidden characters. MAYR (1963) argued that SSC are selectively neutral but influenced by genes that code for selectively important traits. EBERHARD (1985) refuted this hypothesis as it does not explain why (a) only SSC and not somatic characters tend to be affected and (b) primary genitalia are unaffected when sperm transfer is mediated only by secondary genitalia. ARNOLD (1973) proposed a similar hypothesis but assumed that genitalic characters are not neutral but assure species-specific matings by a lock and key mechanism. Whereas EBERHARD's (1985) refutation of the lock and key hypothesis is extensive and convincing, his arguments concerning pleiotropy arè not. It should be obvious that just like other characters, linked traits are subject to selection and will disappear when they are disadvantageous. SSC as well as somatic characters might be affected by pleiotropy linkage, but when these links are not advantageous they are bound to disappear, possibly together with the characters themselves.

FITNESS : THE BEHAVIOURAL COMPONENT

Apart from on its morphological adaptations, the survival of an individual largely depends on its behavioural adaptations. In order to be successful, it has to act in the right way : it should prefer the right habitat, be active at the right time (in the right season, at the right time of the day), show those food preferences that enable it to obtain enough resources and, importantly, behave in such a way as to avoid predators.

As these kinds of adaptations, although crucial for survival, often have no directly obvious morphological expression, the hypothesis suggests that information about their presence is conveyed by SSC (see Fig. 1).
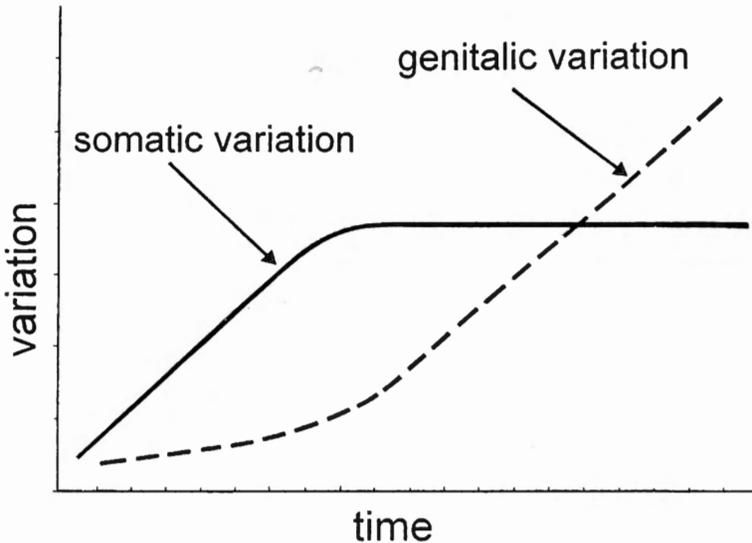

Fig. 1. – Fluctuation of somatic and genitalic variation in time within a particular animal group: a period of strong somatic radiation and relative genitalic stability, is followed by of period of rapid genitalic radiation and stable somatic patterns.

It is evident that in the course of time, as niches become narrower, all these preferences undergo a tendency towards higher specialisation. As the number of species increases and mechanisms of protection of possible resources, plants as well as animal prey items, improve, the need for specialisation undergoes a parallel increase. Together with that increasing specialisation, the amount of information transferred during (pre)mating has to increase. It is clear from phylogenies for certain invertebrate groups (e.g. Araneae, *Tenedos*: JOCQUÉ & BAERT 1996, *Storena*: JOCQUÉ & BAEHR 1992, BAEHR & JOCQUÉ 1994, Lycosoidea: Griswold 1993, Diptera: Mycetophilidae: SÖLI 1997, Pipunculidae: DE MEYER 1995, 1996) that the complexity of genital structures has increased considerably in the course of evolution. This has been explained as a random phenomenon greatly dependent on incidental preferences of females. In the present hypothesis it is argued that when particular characters, behavioural and perhaps morphological, develop, they have to be exteriorised by parallel genital traits. A famous example is that of black-headed male sticklebacks which exhibit flight reaction from particular large fish predators, such reaction being absent in the red-headed males that mainly occur in habitats where these predators are absent. The development of the flight reaction is exteriorised by the development of the appearance of a black head in the male during the breeding season (McPHAIL, 1969). This enables the female to «verify» that a particular male has acquired the flight reaction. Females that choose red-headed males choose a partner that does not have this reaction.

Another example might be found in spiders. In species of the genus *Hortipes,* a recently described genus of African Liocranidae (BOSSELAERS & LEDOUX, 1998), I observed that the males from South African mountain forest species have simple palps whereas a somatically almost identical species from West African lowland forest has much more complex palps although it is not clear yet what particular palpal character is involved. The circumstances in which both these animals live is extremely different, mainly in the numbers of predators encountered (ants, see for instance JOCQUÉ 1984). Observation of live males showed that when disturbed, lowland males jumped about as far as ten times their body length whereas highland males just ran for a short bout not exceeding four times their length. We assume that the flight reaction acquired by the lowland spiders is exteriorised by one of the characters in the (much) more complex palp. In the same genus another example of behavioural adaptation that might be linked to palpal morphology can be found. All representatives of this genus live in the litter layer of evergreen forest except one which was found mainly in grassland surrounded by forest in Natal. That particular species is part of a large clade with many closely related species which are difficult to separate. Although it is evidently part of that clade, it differs from the other species by an unusually large number of autapomorphies. The apparently dramatic change in behaviour that enables this species to live in grassland rather than in forest is assumed to be accompanied by a clear shift in palpal morphology. How the information could be transferred in such a system is not immediately clear but is likely to be mediated by cryptic female choice (see EBERHARD 1996 for a review) which should then be called «mate check». Males that do not have exactly the right behaviour and the exact male palpal morphology linked to it, do not succeed in passing sperm in the right way or to the exact spot in the epigyne and are likely to have their sperm rejected in one way or another. It is inevitable that the female genitalia must provide means to select, in some cases cryptically (EBERHARDT 1996, HUBER & EBERHARDT 1997) the characters of the male genitalia. This explains why in the past, the complementary structures of male and female genitalia have lead to hypotheses such as «lock and key» and mate «recognition».

The question arises whether all newly acquired traits have to be exteriorised by sexual traits. The answer is probably no. Those characters that have a conspicuous morphological expression probably do not require sexual exteriorization as they already play a role in the initial recognition between the sexes and are likely to be automatically checked during the onset of courtship. However, if a particular somatic adaptation is only meaningful in combination with specialised behaviour, it is likely that the behaviour needs back-up of a particular SSC.

LIMITS TO EXTERIORISATION

It is evident that every system that exteriorises specialisation reaches a limit of complexity when niches become narrower and the species more specialised. It is therefore understandable that in many animal groups traits other than purely genital secondary sexual ones have developed. If the sexual organs have reached a limit of complexity, due to structural or evolutionary constraints (see HORNE *et al.* in press), other traits can be added to accompany increased behavioural or morphological complexity. The possibilities

in this respect have been reviewed mainly by EBERHARD (1985). It should be noted though, that certain developments are easily understood in the light of necessary increasing complexity of sexual organs. In spiders for instance, the evolution of the epigyne has increased the possible complexity for the male palp tremendously (examples of haplogyne versus entelegyne). This would mean that the success of a group and its proneness to radiate is highly dependent on the flexibility and the variability of its mating system, which has been called a « copulatory module » (MARTENS, in press). The success of cichlid fishes in great lakes (FRYER 1991, KAUFMAN et al. 1997) may at least partly be explained by fine-tuning of male characters (colour for instance) during courtship. These small colour variations in courting males often appear to be the only morphological differences (SNOEKS 1991, SEEHAUSEN & VAN ALPHEN, 1998) in species that occupy very specialised niches. These however, must be considered the crucial information for the matching females. Males of specialised grazers for instance, advertise their specialised grazing behaviour by their colour which is the only means female have to check the presence of this crucial character. Males with slightly different colour may advertise different grazing behaviour. Although the original meaning of this system is here assumed to check the genetic quality of the male, recognition may be a secondary advantage in mixed populations of strongly related species.

Traits other than morphological ones offer more possibilities for variation and are often those that do not compromise the viability of the males, thus facilitating further specialisation than purely morphological traits would do. Visual, auditive, chemical and even electrical (mormyrid fishes) stimuli offer probably many more possibilities to transfer information than would purely morphological ones. In spiders and insects with good eyesight a good deal of the courtship and thus mate check, is based on visual stimuli. It is probably not a coincidence that precisely those families that rely on such information transfer are among the most speciose (Salticidae, Lycosidae in spiders; Hawaiian Drosophilidae and many other groups in Diptera; Cichlidae in Pisces; birds as a whole).

Auditive information transfer is probably even more efficient as the « sender » can remain concealed while transferring messages. Perfect examples are Passeriformes among birds (with the development of the syrinx), frogs and toads among Amphibia, Orthoptera and Homoptera among the insects. Another possibility is the use of pheromones which have advantages similar to auditive messages. The extremely low concentrations at which these chemicals can be used allow very low population densities. It is clear that chemical information transfer is often used as a complement to tactile and auditive systems: e.g. presence of glands in cephalothorax pits in male Linyphiidae (Araneae) obviously serve to transfer information during copulation. In this family, tactile, auditive and chemical stimuli are used in combination, which is assumed to be an apparent consequence of the narrow niches in which these spiders live, since up to 50 species may occur in the same macrohabitat. Animal groups that use these kinds of information transfer during courtship are likely to be much more flexible as they have a much larger array of possibilities than those that use purely morphological traits and radiations are therefore to be expected in these groups. The efficiency of sex linked information transfer might be crucial in groups that have similar ecological possibilities. The success of Araneidae (Araneae) in comparison with Uloboridae, both of which make orbwebs but with different sticky systems, may

be due to the more flexible SSC of the former rather than to the inferior capturing system of the latter.

PHYSICAL ADAPTATIONS AND FEMALE CHOICE

From the above it is clear that the hypothesised «mate check» is an all or nothing mechanism. The selection by the mate depends entirely on the presence (quality) of the SSC. The SSC, however, are themselves subject to variation and the strength of the SSC varies along a quantitative gradient.

In contrast to behavioural adaptations, physical adaptations can be deduced in the first place from the somatic quality of a partner, its size and strength, in the second place from the quantitative expression of its SSC: their size, intensity of their colour, song intensity etc. If verification of the presence of these characters is important, females may develop an a posteriori attraction to these characters and should thus be stimulated by their presence. It is then evident that the more developed is the secondary sexual trait, the stronger will be the signal and the easier will be the verification by the female partner. It is therefore only reasonable that females, if given the opportunity, choose the male with the strongest signal. Female choice could therefore be considered a secondary effect of «mate check».

Secondary sexual characters are likely to vary quantitatively, just as for instance the size of an (r-selected invertebrate) organism does. The stability of size is a very similar phenomenon: although larger females have an advantage as larger size enables larger clutches, size remains stable around a certain average, simply because there is a strong feedback as size tends to be a significant adaptive trait, and small females may have a strong advantage in adverse conditions. Likewise, secondary sexual characters may vary to a certain extent, but, for the same reasons, fluctuate around a fixed average. The strength of the male signal exerted by SSC is a result of genetic and phenotypic variations (Fig. 2) as are size and the quality of other morphological characters. It is easily understood that in a purely theoretical condition, when all circumstances are optimal (here shown as optimal habitat quality) all variation is due to the genetic component. When however, the quality of the environment decreases, the phenotypic component increases in importance. The variation as a whole is the sum of both genetic and phenotypic variation.

The result of this phenomenon, the quantity aspect, which explains the cases in which brighter, larger etc. characters are favoured as they reflect the physical component of fitness, has been misinterpreted as the driving force behind the development of SSC. A weakness of these hypotheses is indeed that they have rarely made a clear distinction between the qualitative (presence) and quantitative (expression) aspects of SSC and consider their acquisition a result of exaggerated quantitative traits. In practice it is extremely difficult to separate the phenotypic and genotypic component of the quantity of SSC. For practical reasons, observations and experiments are mainly carried out in near optimal conditions, and thus it is likely that the observed heritability is biased since it may be expected to be higher than average in these conditions. It is therefore important that the entire population is considered, including those individuals that live in marginal conditions.

genetic + phenotypic variation

male signal strength

genetic variation

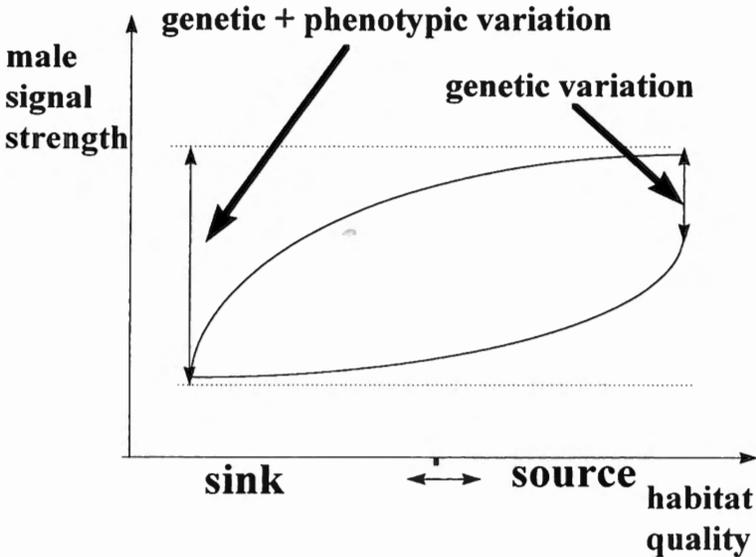**sink ←→ source** habitat quality

Fig. 2. – Variation of intensity of the signal of male secondary sexual characters. In a purely theoretical condition, when all circumstances are optimal (here shown as optimal habitat quality) all variation is due to the genetic component. When however, the quality of the environment decreases, the phenotypic component increases in importance. The variation as a whole is the sum of both genetic and phenotypic variation. It is assumed here that speciation events occur in the lower reaches of the environmental gradient and not in its upper part as implied by the female choice hypothesis.

If the development of an SSC is the result of runaway evolution or of an indicator mechanism, there should be a very unstable situation. One of the predictions of female choice (EBERHARD 1985) is indeed that SSC should be highly variable as males would be involved in an arms race to acquire SSC with as strong a signal as possible. However, HUBER (1996) and mainly EBERHARD *et al.* (1998) have shown that secondary genitalia and other SSC in insects and arachnids tend to be more stable than somatic characters. It thus appears that, at least in organisms with what they call « cryptic female choice » (EBERHARD 1996), the mechanism involved is a precise « mate check » rather than female choice. In organisms with « overt choice » (in contrast to « cryptic choice »), SSC do indeed strongly fluctuate around a certain average. Here again, a distinction should be made between quality (presence) and quantity (expression) of SSC. Once a new SSC (a new « quality ») is acquired, the strength of its signal will fluctuate (quantitatively) around a certain average and remain stable around that average. This is in concordance with the punctuated equilibrium theory (ELDREDGE & GOULD 1972, GOULD & ELDREDGE 1986), which states that most species tend to be stable for a relatively long period in geological time. So female choice must be considered the result of the evolution of SSC and not their origin. The presence of an SSC increases the possibility for females to choose between signals of different strength. In cases with overt choice, SSC indeed provide much better possibilities for

sexual selection than purely somatic characters alone would do, since the degree of expression of SSC, hence their signal strength, appears to be quantitatively more prone to variation than other characters. MØLLER & POMIANKOWSKI (1993) provide evidence that the patterns in fluctuating asymmetry for SSC, differ from those in somatic traits and that the former show much higher levels of fluctuating asymmetry.

The difference between the two types of choice, overt or cryptic, prompts another comment : in organisms that apply overt choice, primarily vertebrates, and on which most of the literature on sexual selection is based, the influence of the SSC themselves may often be obscured, mixed as it is with many other influences especially the mate's complex behaviour. Particularly in vertebrates, behavioural adaptations cannot always be considered as hidden. During the intensive interaction between mates, even outside the mating process, females may be able to interpret the adaptive quality of the male's behaviour so that the need for exteriorisation is lower. In animals with cryptic choice on the other hand, contact between mates is often very superficial and of very short duration if occurring at all. A perfect example are those taxa in which there is no copulation and sperm transfer is mediated by spermatophores, that may vary to a great extent (e.g. Pseudoscorpiones; Amblypygi) (WEYGOLDT 1969, WEYGOLDT & HOFFMANN, 1998). In these circumstances there is no appreciation possible of the male's behaviour and any information about it is has to be transferred via the spermatophore. Similar considerations apply to most invertebrates that only meet during copulation. For these reasons, the importance of « mate check » will be much more difficult to demonstrate in « higher » animals than it will be in invertebrates.

ARNQVIST (1998) recently argued that complex SSC are obviously the result of female choice as monandrous invertebrates appear to have much more simple SSC than do polyandrous species. The greater possibility for the females of the latter category to really choose, is supposed to increase the tendency to radiation. Apart from the fact that this mechanism cannot explain the evolution of complex spermatophores, the main question in this context has not been formulated. Since mating is a very costly activity requiring a high amount of time and energy, and considerably increases the risk of being detected by a predator, it should be questioned why some species do mate more than once while others do not? The answer may be found precisely in the correlation detected by ARNQVIST (1998), which also works the other way round. If SSC become more complex with specialisation, it is conceivable that the risk of unsuccessful matings increases accordingly. Multiple matings would therefore become a necessity to keep the risk of remaining unfertilised low, and polyandry could then be considered as an inevitable drawback of high specialisation.

MATE CHECK AND THE ENVIRONMENT

It has been shown several times that the quality of male ornaments is linked to breeding success and to survival rate of the offspring (already mentioned by WALLACE 1889, ANDERSSON 1994 :26, WILLIAMS 1975, 1992, PETRIE 1992, 1994, MØLLER 1994).

It may be questioned, however, whether the observed survival rate is only a question of correct mate choice. Little attention has been paid to the effect of the environment on the

incidence and thoroughness of mate choice. In marginal habitats or in bottle-neck situations it is very likely that females are much less fastidious (Fig. 3) than they would be in more advantageous circumstances. The risk of remaining uninseminated might increase considerably in cases of low population density. Time investment in courting may also become risky if resources are scanty and time needed to acquire them is high. It is therefore not unlikely that females which have grown up in favourable conditions, are much more choosy and that the high survival rate of their offspring is mainly due to their own condition and less to the quality of the male as advertised by the quantitative expression of the male's SSC.
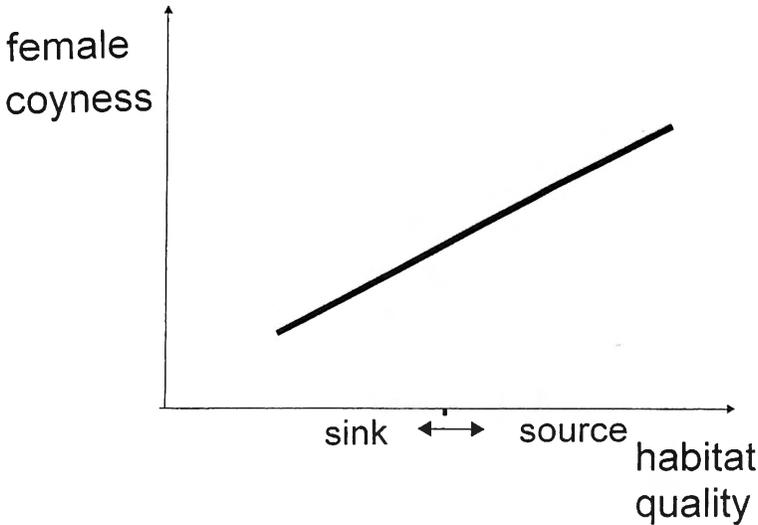

Fig. 3. – Variation of female coyness in respect to the selection of males. In a marginal environment (sink) the female will be less choosy as both the risk to remain unfertilised and the time needed to acquire resources increase and less energy may be invested in courtship-related activities.

Selection for a strongly developed secondary sexual trait does not select for an adaptive character but for the physical fitness component, and there is an increasing amount of evidence that this type of fitness is not heritable (GUSTAFSSON 1986; SMITH 1988; WILLIAMS 1975, 1992).

It may be argued that « mate check » is identical to the « good genes » hypothesis. The main difference between these hypotheses is that mate check is an « all or nothing » (qualitative) mechanism that also works in marginal habitats or bottle neck circumstances whereas « good genes » is a quantitative mechanism in which the driving force is female selection of the strongest male signal. As the strength of the male signal is the result of both genetic and phenotypic influences, the quality of the genes might be masked by phenotypic regression. This means that the « good genes » model proposes a risky mechanism that might jeopardise breeding in adverse conditions. « Mate check » on the other hand remains efficient in any circumstances. Another difference is that « mate check » assumes

a link between particular behavioural characters that have been acquired in the recent evolution and the SSC of the taxon whereas «good genes» assumes a random effect, reflecting overall fitness. «Mate check» can therefore be expected to generate different levels of complexity whereas «good genes» does not. «Good genes» does not explain the regression of SSC in cases of ecological relaxation nor the rapid decline of species in conditions where «checking the mate» becomes difficult. However, HURST & POMIANKOWSKI (1998) and WILKINSON *et al.* (1998) provide a new interpretation of the «good genes» model. According to their data, female choice selects a male SSC (in this case long eye span of Diopsidae flies) that is linked with a meiotic drive suppressing gene. Although it is not clear how common the phenomenon of meiotic drive might be, it shows that the idea according to which females assess general male viability is certainly not universal.

Another consequence of the reasoning behind female choice is that speciation would mainly occur at the top end of the habitat gradient, where female choice is highly selective. This hypothesis does not take into account the environmental conditions involved in speciation. It is much more likely that speciation occurs at the lower end of the gradient, in marginal habitats or sinks where resources are much less efficiently exploited than at the other extreme. The acquisition of a new (behavioural) character might enable the new species to exploit the resources more efficiently and thus become established. The development of a new SSC that backs up the newly acquired adaptation is hypothesised to be crucial for its consolidation.

For all these reasons it would seem that many of the studies that have tried to show that sexual selection favours the evolution of SSC (e.g. ALATALO *et al.* 1991 ; PETRIE 1992, 1994) have focused on the wrong aspect. It is also important to note that most of the experiments and observations that have studied female choice and its influence on survival of offspring were done in the upper environmental gradient. In this part of the gradient, the genetic component that influences the quantity of SSC is assumed to be higher than the phenotypic component. In the lower reaches of the gradient the latter will be of much higher importance and may help to explain why SSC vary around a certain average.

On the other hand, relevant studies are those that have linked changes in the set of SSC to radiations or to changes in the environment. The studies on cichlids (Pisces) in the African great lakes are well documented in this respect (SEEHAUSEN *et al.* 1997, GALIS & METZ 1998).

An obvious question that arises when one examines the present hypothesis is the following : if the mechanism has evolved mainly as a system to avoid the loss of crucial behavioural adaptations, would it not be logical to expect that males that have undergone such a deleterious mutation would not survive to adulthood, thus rendering the mechanism meaningless? Populations live in a highly variable environment, both in space and time. Some populations or parts of them unavoidably occur in marginal habitats and, more importantly, they are regularly subjected to periods of environmental stress, witnessed by the frequent extinction of isolated populations (MAC ARTHUR & WILSON 1967). Poorly adapted males might survive optimal conditions and thus take part in the reproductive process, but be rapidly exterminated as soon as conditions become critical. The offspring of females that have accepted a male without the crucial adaptations may thrive as long as the conditions stay favourable, but go extinct when they become adverse. The offspring of those females that have checked their mates more efficiently, will have a much higher chance for survival in bottle neck conditions (WIENS 1979).

Another problem for the « mate check » hypothesis is the following. If checking the hidden adaptive qualities of the male is of primary importance for the female, why is it not as important for the male to check the female? The answer to this question should not be fundamentally different from the one proposed in other hypotheses for the evolution of complex animal SSC (see ANDERSSON 1994). The competition for females between males is apparently so strong that it would be a risky strategy for males to build-in a system that restricts the females with which they can mate. Finding a receptive female is likely to be of utmost importance, and restricting the possibilities is likely to be counterproductive in any sense of the word.
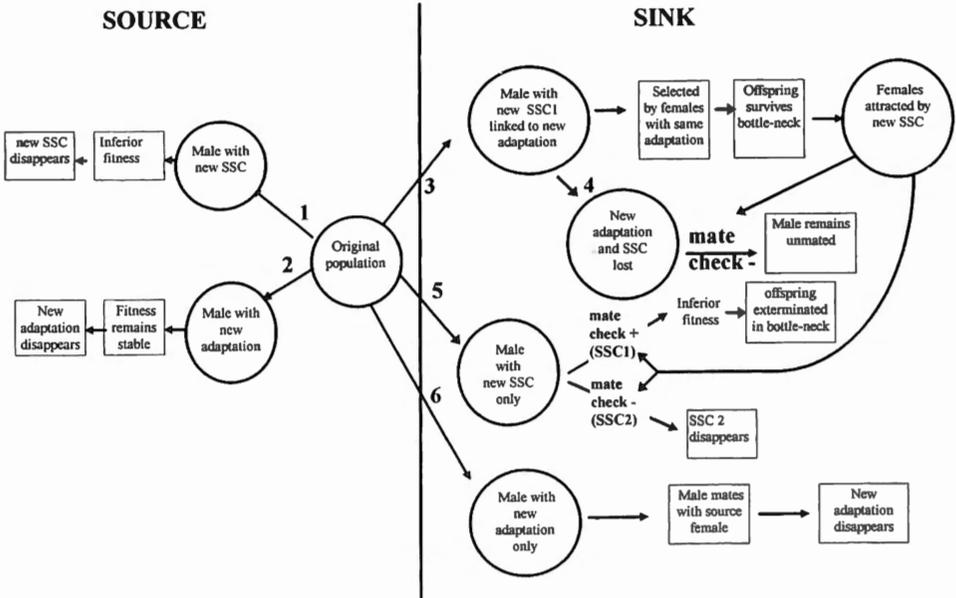

Fig. 4. – A possible scenario of the way in which mate check arises and operates. Circles represent individuals, boxes events and mechanisms. The original population is well adapted to the source situation. New SSC (pathway 1) will increase the males' handicap without compensation in fitness and will soon disappear. New adaptations (pathway 2) have no significant effect on the fitness which remains stable. In the sink situation on the other hand, individuals with a new adaptation are able to exploit resources in circumstances that are marginal for the original population. This is what happens in pathway 3: males with both the new adaptation and SSC1 linked to it, are selected by females with the same adaptation. Their offspring is able to survive the adverse conditions the members of the original population could not. Females become a posteriori attracted and/or stimulated by the new SSC1 of the male. From this stage on, males are checked for the presence of SSC1. In pathway 4, the new adaptation and SSC1 have been lost and males remain unmated since not accepted by mate check. In pathway 5, males acquire a new SSC. If it is SSC1, exactly the same as the one linked to the new adaptation mate check will have a positive outcome but the offspring will not survive an environmental bottle neck situation and disappear. In case it is another SSC, mate check has a negative outcome and SSC2 disappears.
Pathway 6 presents what might happen before the evolution of SSC1 and the connected mate check. Males with the new adaptation mate with source females and the character disappears . Once « mate check » for SSC1 has evolved, this pathway follows the same course as 4.

CONSEQUENCES AND PREDICTIONS

As the complexity of the SSC is hypothesised to be linked to specialisation, one should expect that in similar representatives of a particular guild, the groups with small-sized representatives would have more complex SSC than would representatives of large size. The simple reason is that the smaller the organisms, the higher the habitat specialisation may be. Good examples are Paradoxosomatidae (HOFFMAN & HOWELL 1985), tiny diplopods which have particularly complex genitalia, Linyphiidae (and some other spider families with tiny representatives) which have a large array of SSC on top of very complex secondary genitalia, Membracidae (Homoptera) with complex appendages, Mycetophilidae (Diptera), Passeriformes in birds which have enormous possibilities thanks to the development of the syrinx (RAIKOW 1986, 1988) and barbs (Barbus) and cichlids, mainly in African lakes.

The above hypothesis inevitably results in a time sequence. In the course of time, as niches become narrower and species more specialised, genitalia are assumed to have gone through a parallel evolution of increasing complexity. The organisms that have survived are those that have evolved systems that enable enough information transfer to match the acquired specialisation. It is likely that in certain circumstances (after global disasters, colonisation of underpopulated areas) a certain regression has occurred which may explain instances in which a general decrease in complexity of SSC has occurred.

If we accept that SSC complexity is related to specialisation we may indeed expect a reversible mechanism. If for one reason or another a population undergoes ecological relaxation it should be possible that its sexual characters become equally simple. A few observations point indeed in that direction. KANESHIRO (1983) reports on a case in Hawaiian drosophilids that colonised a new island; courtship in the species is simplified because the receptivity threshold of females is lowered. The same phenomenon was observed in populations of *Drosophila adiastola* that were kept in captivity. After a number of generations the highly specialised species showed simplification of its courtship. In both cases the phenomenon can be explained by a decrease in ecological specialisation paralleled by a decrease of courtship complexity. Hawaiian drosophilid species are highly specialised and each lives on very restricted resources which implies a highly typical behaviour. When individuals are transferred to different ecological circumstances or kept in captivity, resources are bound to be more readily available to them, the species' behaviour less characteristic and complex, and the amount of information to be transferred during courtship equally less complex. In his monumental review of the subject, ANDERSSON (1994) states that « the roles of ecological divergence and sexual selection in these speciations therefore are hard to disentangle ». If however, the present hypothesis proves correct, they are not entangled at all but should be perfectly linked.

Another well known example is the occurrence of drabness in island birds. Birds with brightly coloured males often tend to become much more drab after colonising an island. In the light of the present hypothesis this should be understood as the result of the occupation of a less specialised niche. The number of predators may be lower, the food resources more diverse and hence the behaviour of the birds different, and less specialised, from that of the source population. The amount of information to be transferred to the

females is lower and certain secondary traits might be lost. As auditive messages are probably the primary information carriers among sexes (CATCHPOLE 1987) and colourful plumage is only adopted in highly specialised species, it would not be surprising that the first shifts in island colonisers are to be found in the colour of their plumage (GRANT 1965, LACK 1968).

But the reverse is also possible: ecological specialisation might be lost as a result of less efficient mate verification. In some cichlid groups in Lake Victoria, many particularly specialised species disappeared as a result of eutrophication (SEEHAUSEN et al. 1997). In these fishes mate check is supposed to be based mainly on male colour pattern. As the visibility and the possibilities for recognition of the colour pattern decreased with increased turbidity, many specialised species that are here assumed to be maintained by mate check, disappeared. In this example the selection primarily maintains reproductive isolation between closely related, highly specialised species that live in sympatry. However, the mechanism is equally crucial for highly specialised species that live in isolation. Interesting examples in this respect are the studies on cave spiders with complex genitalia (BOSSELAERS 1998, WEISS & HEIMER 1982). The latter authors described two cave spiders with very complex secondary genitalia. They express their confusion about these apparently useless organs as these species live in perfect isolation in different parts of the cave. In the light of the present hypothesis it could mean though, that the complex genitalia exteriorize the strong specialisation connected to troglobitism.

The supposed exteriorization of behavioural characters is likely to be hierarchical. Only those characters that are not automatically linked with the morphology of the species have to be exteriorized. Cichlids that graze algae do not need special SSC as their morphology compels them to do so. However, the behaviour that regulates on what kind of substrate, what depth and in what other circumstances they graze, does need exteriorization. Only behavioural characters that present a shift from the ordinary original behaviour do need exteriorization. Therefore, a system that allows a species to get rid of exteriorization of old characters that are supported by the morphology itself, is particularly flexible and bound to be successful. The statement of Lande (1981) that the evolution of a new SSC may contribute to the decline of an old one must be seen in this perspective.

MATE CHECK AND PHYLOGENY

A possibility to test the present hypothesis is provided by the following: if the hypothesis is correct there should be a correlation between the complexity of the behaviour and the soma on the one hand and that of the genitalia on the other hand. However, in some well studied spider taxa (Araneae Lycosoidea: GRISWOLD 1993, ZODARIIDAE: JOCQUÉ 1990, JOCQUÉ & BAEHR 1992, BAEHR & JOCQUÉ 1994, 1996, JOCQUÉ & BAERT 1996), there is no such clear correlation between somatic and genitalic complexity at generic level. There is evidence that an early split-up into very different somatic patterns (genera) occurred while the SSC remained fairly simple. Afterwards the genera radiated into many similar species in which the somatic pattern remained stable but the SSC became sometimes spectacularly complex (GRISWOLD 1993, JOCQUÉ & BAEHR 1992, JOCQUÉ 1990, BAEHR & JOCQUÉ 1994, 1996, JOCQUÉ & BAERT 1996, BOSSELAERS & JOCQUÉ, in prepara-

tion). This phenomenon may be the result of an initially easy adaptation with large somatic differences which did not need highly sophisticated SSC. Much of the information transfer was achieved simply by recognition of purely somatic characters. Once these many different basic patterns had been established, further specialisation was mainly achieved by behavioural adaptations. This statement would indicate that mate check is in the first place a mechanism to verify behavioural adaptations and that strong specialisation based on highly specialised behaviour is to be backed by increasingly complex SSC.

As pointed out above, the increase in complexity of the male SSC must be seen in the light of mainly behavioural traits as somatic changes are not necessarily accompanied by changes in the SSC. Within a large clade with stable somatic morphology as in the examples mentioned above, the increase in complexity of the SSC is supposed to be an answer to increasingly specialised niches. As these become narrower with time, it should be assumed that the species with simple SSC, the most plesiomorphic taxa, have gone extinct or become very rare and should only be found in relict habitats. The most derived taxa on the other hand should also be rare as they are supposed to be highly specialised and only occur in very narrow niches. The most widespread species should therefore be found in the intermediate taxa. I therefore assume there must be a relationship between the degree of apomorphy (derivedness) of the SSC and the distribution area of the species.

MATE CHECK AND SPECIATION

Apart from speciation by genetic drift which is proven for instance by the existence of ring-species, a probably more common type of speciation occurs by the acquisition of new traits, behavioural or morphological novelties. That kind of speciation is bound to happen in « sinks » (marginal habitats) (DIAS 1996) where the selection by females is less severe. A mutation that allows more efficient exploitation of the sink's resources, through a change of morphology and/or behaviour, is exteriorised by a sexual trait. Only if both these conditions are fulfilled is there a possibility for the new adaptation to be selected for and to be consolidated in later generations. The original species is likely to become less abundant in, or disappear from the sink as it lacks the necessary adaptation to exploit its resources as efficiently as the new species. The chance that this happens is highly dependent on niche pressure (JOCQUÉ, 1982), the extent to which the resources in the sink are underexploited. There is a fundamental difference in both types of speciation: in the former, often the result of geographical isolation, the complexity of the SSC does not have to change as the degree of adaptation remains similar. In the second type of speciation on the other hand, the newly acquired characters will need a parallel increase in the complexity of the SSC.

Slight changes in the extent of an SSC have often been interpreted as reinforcement; in the presence of a closely related species, SSC's would be emphasised in order to enhance the species' isolation. In the light of the present hypothesis this should rather be seen as a result of the optimal circumstances in which the species live. The fact that only one of a closely related pair of species is able to occupy a particular habitat indicates that the resources are limited. The SSC will then be less pronounced and show average diffe-

rences in a situation where resources are so abundant that closely related species are able to cohabit.

CONCLUSIONS

In contrast to the classical female choice hypotheses, mate check can explain why species are stable; it also explains why particular taxa are prone to radiate whereas others are not; mate check further explains why in some species SSC are complex, and may be so even in species living in isolation, whereas they are simple in many others.

The present hypothesis might eventually provide the answer to the old question «what comes first in a speciation event, the adaptive character that enables a new species to profit from underexploited resources or the SSC that characterises the species?». The answer is that they both occur at the same time and that, at least a behavioural novelty has to be backed up by a SSC, otherwise it can't be consolidated.

In the present context it would seem that female choice is not a special separate mechanism accelerating radiation, but is a result of mate check.

ACKNOWLEDGEMENTS

REFERENCES

ALATALO, R.V., J. HÖGLUND & A. LUNDBERG (1991) – Lekking in the black grouse – a test of male viability. *Nature*, **352**: 155-156.

ANDERSSON, M. (1994) – *Sexual selection*. Princeton University Press. Princeton , New Jersey, 599 p.

ANDERSSON, M. & Y. IWASA (1996) – Sexual selection. *Trends in ecology and evolution.* **11** : 53-58.

ARNOLD, E.N. (1973) – Relationships of the palaearctic lizards assigned to the genera *Lacerta, Algyroides* and *Psammodromus* (Reptilia : Lacertidae). *Bull. Br. Mus. Nat. Hist. (Zool.)*, **25** : 291-366.

ARNQVIST, G. (1997) – The evolution of animal genitalia : distinguishing between hypotheses by single species studies. *Biol. J. Linn. Soc.*, **60** : 365-379.

ARNQVIST, G. (1998) – Comparative evidence for the evolution of genitalia by sexual selection. – Nature, **393** : 784-786.

BAEHR, B. & R. JOCQUÉ (1994) – Phylogeny and zoogeography of the Australian genus *Storena* (Araneae, Zodariidae). *Spixiana*, **17** : 1-12.

BAEHR, B. & R. JOCQUÉ (1996) – A revision of *Asteron,* starring male palpal morphology. *Revue Suisse Zool.* hors série : 15-28.

BOSSELAERS, J. (1998) – *Nesticus henderickxi* (Araneae, Nesticidae), a new blind troglobitic spider from Crete. *Bull. Br. Arachnol. Soc.*, **11** : 9-14.

BOSSELAERS, J. & J.-C. LEDOUX (1998) – Description of a new African genus, *Hortipes* (Araneae, Liocranidae). *Revue Arachnol.*, **12** : 147-152.

CATCHPOLE, C.K. (1987) – Bird song, sexual selection and female choice. *TREE*, **2** : 94-97.

DARWIN, C. (1859) – *The origin of species*. London, J. Murray.

DARWIN, C. (1871) – *The descent of man and selection in relation to sex*. London, J. Murray.

DE MEYER, M. (1995) – The pipunculid flies of Israel and the Sinai. *Spixiana*, **18** : 283-319.

DE MEYER, M. (1996) – Cladistic and biogeographic analyses of Hawaiian Pipunculidae (Diptera) revisited. *Cladistics*, **12** : 291-303.

DIAS, P. (1996) – Sources and sinks in population biology. *TREE*, **11** :326-330.

EBERHARD, W.G. (1985) – *Sexual selection and animal genitalia*. Harvard University Press. Cambridge, Massachussets. 231 p.

EBERHARD, W.G. (1996) – *Female control : sexual selection by cryptic female choice*. Princeton University Press, Chichester, West Sussex.

EBERHARD, W., B. HUBER B. , R. RODIGUEZ, R. BRICENO, I. SALAS & V. RODRIGUEZ (1998) – One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution*, **52** : 415-431.

ELDREDGE N. & S. GOULD (1972) – Punctuated equilibria : an alternative to phyletic gradualism. In : Ed. Schopf, T. *Models in Palaeobiology*. Freeman, Cooper & Co. San Francisco, 82-115.

FISHER, R.A. (1930) –.*The genetical theory of natural selection*. Clarendon Press, Oxford, 272p.

FRYER, G. (1991) – The evolutionary biology of African cichlid fishes. *Ann. Mus. r. Afr. Centr. Sc. Zool.*, **262** : 13-22.

GALIS, F. & J. METZ (1998) – Why are there so many cichlid species? *TREE*, **13** : 1-2.

GOULD, S. & N. ELDREDGE (1986) – Punctuated equilibrium at the third stage. *Syst. Zool.*, **35** : 145-148.

GRAFEN, A. (1990) – Sexual selection unhandicapped by the Fisher porcess. *J. theor. Biol.*, **144** : 473-516.

GRANT, P.R. (1965) – Plumage and the evolution of birds on islands. *Syst. Zool.*, **14** : 47-52.

GRISWOLD, C. (1993) – Investigations into the phylogeny of the lycosoid spiders and their kin. (Arachnida : Araneae : Lycosoidea). *Smithson. Cont. Zool.*, **539** : 1-39.

GUSTAFSSON, L. (1986) – Lifetime reproductive success and heritability : empirical support of Fisher's fundamental theorem. *Am. Nat.*, **128** : 761-764.

HEYWOOD, J. (1989) – Sexual selection by the handicap mechanism. *Evolution*, **43** : 1387-1397.

HOFFMAN, R. & K. HOWELL (1985) – A new Tanzanian genus of paradoxosomatid millipeds with medusiform gonopods (Diplopoda : Paradoxosomatidae). *Revue Zool. afr.*, **99** : 57-61.

HORNE D.J., D.L. DANIELOPOL & K. MARTENS (in press) – Reproductive behaviour. *In:* MARTENS K. (ed.) *Sex and parthenogenesis: evolutionary ecology of reproductive modes in non-marine ostracods* : 157-196. Backhuys, Leiden.

HUBER, B. (1996) – Genitalia, fluctuating asymmetry and patterns of sexual selection in *Physocyclus globosus* (Araneae, Pholcidae). *Rev. Suisse Zool.* hors série : 289-294.

HUBER B. & W. EBERHARD (1997) – Courtship, copulation and genital mechaninism in *Physocyclus globosus* (Araneae, Pholcidae). *Can. J. Zool.*, **75** : 905-918.

HURST, L.D. & A. POMIANKOWSKI (1998) – The eyes have it. *Nature*, **391** : 223-224.

JOCQUÉ, R. (1982) – Niche Pressure and the optimum exploitation hypothesis. *Biol. Jb. Dodonaea*, **50**: 168-181.

JOCQUÉ, R. (1984) – Considérations concernant l'abondance relative des araignées errantes et des araignées à toile vivant au niveau du sol. *Revue Arachnol.*, **5**: 193-204.

JOCQUÉ, R. (1990) – A revision of the afrotropical genus *Diores* (Araneae, Zodariidae). – *Annales Mus. R. Afr. Centr.* **260**: 1-81.

JOCQUÉ, R. & B. BAEHR (1992) – A revision of the Australian spider genus *Storena* (Araneae, Zodariidae). *Invert. Taxon.*, **6**: 953-1004.

JOCQUÉ, R. & L. BAERT (1996) – *Tenedos*, an early conquest of America. *Revue Suisse Zool.* hors série: 309-320.

KANESHIRO, K.Y. (1983) – Sexual selection and direction of evolution in the biosystematics of Hawaiian Drosophilidae. *Ann. Rev. Entomol.*, **28**: 161-178.

KAUFMAN, L.S., L.J. CHAPMAN & C.A. CHAPMAN (1997) – Evolution in fast forward: haplochromine fishes of the Lake Victoria region. *Endeavour*, **21**: 23-30.

KIRKPATRICK, M. (1985) – Evolution of female choice and male parental investment in polygynous species: the demise of the «sexy son». *Am. Nat.*, **125**: 788-810.

KIRKPATRICK, M. (1987) – The evolutionary forces acting on female mate preferences in polygynous animals. In: Eds. Bradbury, J.W. & M.B. Anderson *Sexual selection: Testing the alternatives.* 67–82. Wiley, Chichester.

KOCHMER, J.P. & R.H. WAGNER (1988) – Why are there so many kinds of passerine birds? Because they are small. A reply to Raikov. *Syst. Zool.*, **37**: 68-69.

LACK, D. (1968) – *Ecological adpatations for breeding birds.* Methuen. London.

LANDE, R. (1981) – Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA*, **78**: 3721-3725.

MAC ARTHUR, R.H. & E.O. WILSON (1967) – *The theory of island biogeography.* Princeton University Press, 203 pp.

McPHAIL, J.D. (1969) – Predation and the evolution of a stickleback (*Gasterosteus*). *J. Fish. Res. Bd. Canada*, **26**: 3183-3208.

MARTENS, K. (in press) – On the origin and development of different recognition systems in the limnocytherinae (Crustacea, Ostracoda, Cytherocopina): chance or selection? *In:* HORNE, D.J. & MARTENS K. (eds.), Proc. 13 Int. Symp. Ostracodologists. *Hydrobiologia.*

MAYR, E (1963) – *Animal species and evolution.* Harvard University Press, Cambridge, Massachussets.

MØLLER, A.P. (1994) – *Sexual selection and the barn swallow.* Oxford series in Ecology and Evolution. Oxford University Press, 365 pp.

MØLLER, A. & A. POMIANKOWSKI (1993) – Fluctuating asymmetry and sexual selection. *Genetica*, **89**: 267-279.

OTTO, S.P. & Y. MICHALAKIS (1998) – The evolution of recombination in changing environments. *TREE*, **13**: 145-151.

PETRIE, M. (1992) – Peacocks with low mating success are more likely to suffer predation. *Anim. Behav.*, **43**: 173-175.

PETRIE, M. (1994) – Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, **37**: 598-599.

RAIKOW, R.J. (1986) – Why are there so many kinds of passerine birds? *Syst. Zool.*, **35**: 255-259.

RAIKOW, R.J. (1988) – The analysis of evolutionary success. *Syst. Zool.* **37**: 76-79.

RYAN, M.J. (1990) – Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus. Evolution*, **37** : 261-272.

RYAN, M.J., J.H. FOX, W. WILCZYNSKI & A.S. RAND (1990) – Sexual seletion for sensory exploitation in the frog *Physalaemus pustulosus. Nature*, **343** : 66-67.

RYAN, M.J. & A. KEDDY-HECTOR (1992) – Directional patterns of female mate choice and the role of sensory biases. *Am. Nat.* S4-S35.

SEEHAUSEN, O., J. VAN ALPHEN & F. WITTE (1997) – Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, **277** : 1808-1811.

SEEHAUSEN, O. & J. VAN ALPHEN (1998) – The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei*) complex. *Behav. Ecol. Sociobiol.*, **42** : 1-8.

SMITH, J.N.M. (1988) – Determinants of lifetime reproductive success in the song sparrow. In : ed. T.H. CLUTTON-BROCK. *Reproductive success*, 154-172. University of Chicago Press, Chicago.

SNOEKS, J. (1991) – The use of a standard colour guide and subtle morphological difference in Lake Kivu haplochromine taxonomy. *Ann. Mus. r. Afr. Centr. Sc. Zool.*, **262** : 103-108.

SÖLI, G. (1997) – The adult morphology of Mycetophilidae (s.str.), with a tentative phylogeny of the family (Diptera, Sciaroidea). *Ent. scand. Suppl.*, **50** : 5-55.

WEISS, I. & S. HEIMER (1982) – Zwei neue *Carpathonesticus*-Arten aus Rumänien nebst betrachtungen über Kopulationsmechanismen und deren Evolution. *Reichenbachia*, **20** :167-174.

WEYGOLDT, . (1969) – *The biology of Pseudoscorpions*. Harvard University Press. Cambridge, Massachussets. 145 p.

WEYGOLDT, P. & P. HOFFMANN (1995) – Reproductive behaviour, spermatophores and female genitalia in the whip spiders *Damon diadema* (Simon, 1876), *Phrynichus* cf. *ceylonicus* (C.L. Koch, 1843) and *Euphrynichus alluaudi* (Simon, 1936)(Chelicerata : Amblypygi). *Zool. Anz.* 234 : 1-18.

WIENS, J.A. (1979) – On competition and variable environments. *Am. Sci.*, **65** : 590-597.

WILKINSON, G.S., D.C. PRESGRAVES & L. CRYMES (1998) – Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. *Nature*, **391** : 276-279.

WILLIAMS, G.C. (1975) – *Sex and evolution*. Princeton University Press., Princeton, New Jersey.

WILLIAMS, G.C. (1992) – *Natural selection : Domains, levels and challenges*. Oxford University Press. Oxford.

ZAHAVI, A. (1975) - Mate selection, - a selection for a handicap. *J. theor. Biol.*, **53** : 205-214.

ZAHAVI, A. (1987) - The theory of signal selection and some of its implications. In : Ed. DELFINA, V.P. *International symposium of Biological Evolution*. Adriatic editrice, Bari. 305-327.

ZEYL, C. & G. BELL (1997) – The advantage of sex in evolving yeast populations. *Nature*, **388** : 465-467.