

Animal personality and sexual selection

Bachelor thesis

Author:

Supervisors:

Second reviewer:

Bachelor project:

Michelle Verreij

s1947338

Franjo Weissing

Piet van den Berg

Ton Groothuis

Gedragsbiologie research

Abstract

Animal personalities, inter-individual differences in behaviour that are consistent across context and across time, have been found in a large range of taxa. Several evolutionary explanations for animal personality have been offered, but little research has focused on the potential role of sexual selection. The aim of this thesis is to investigate the potential role of sexual selection, specifically female mate choice, in the emergence and maintenance of animal personality and to investigate how animal personality, in turn, might influence processes of sexual selection. First, I give a number of examples demonstrating that male variation in behaviour is widespread. Subsequently, I show how female preference might emerge and how female preference can lead to the emergence of quantitative and qualitative variation in male behaviour. Then, I discuss how variation in male behaviour results in differences in compatibility with females. This leads to variation in female preference, of which I give examples. Finally, I address how variation in female preference maintains or even intensifies male variation in behaviour. In conclusion, female mate choice influences the emergence and maintenance of animal personality in several ways. Therefore, when studying animal personality it should be considered whether (and, if so, how) sexual selection plays a part in generating behavioural variation. Animal personality also affect processes of sexual selection. Consequently, when studying intersexual selection, personality differences, both in females and males, should be taken into account where relevant.

Table of contents

Introduction	3
Variation in male behaviour	5
Emergence of female preference and its effect on male variation	7
Emergence of female preference	7
Effect of female preference on male variation	7
Arms race between males	9
Trade-off between adapting to natural selection or sexual selection	9
Emergence of variation in female preference	11
Emergence of variation in female preference	11
<i>Direct benefits and indirect benefits</i>	11
<i>Assortative and disassortative mating</i>	12
Variation in female preference	13
Variation in female preference maintains variation in male behaviour	14
Conclusion & Discussion	16
References	18

Introduction

In the study of animal behaviour an increasing interest in animal personality, also known as behavioural syndromes (Sih et al., 2004a,b; Sih & Bell, 2008), coping styles (Koolhaas et al., 1999), temperaments (Boissy, 1995; Réale et al., 2007) or personality differences (Gosling, 2001), can be observed. The term 'animal personality' refers to individual differences in behaviour that are consistent across contexts and over time (Stamps & Groothuis, 2010). Such behavioural syndromes can be found in a large range of taxa, including fish (Huntingford, 1976), reptiles (Sinervo et al., 2000a), mammals (Koolhaas et al., 1999) and birds (Verbeek, et al., 1996). For instance, in the great tit, individuals show consistent individual variation in open field behaviour. The observed behavioural variation is heritable and can be seen in the wild (Dingemanse et al., 2002) as well as in captivity (Groothuis & Carere, 2005). Additionally, a positive correlation between exploration behaviour and aggression towards conspecifics has been found in the great tit (Verbeek et al., 1996, Groothuis & Carere, 2005), indicating consistency across contexts. Also, individuals of selection lines, selected for fast and slow exploration, differ in exploration in both the juvenile phase and adulthood, pointing toward consistency across time (Carere et al., 2005).

The existence of animal personalities remains difficult to explain from an evolutionary perspective, despite the great attention and study it has received in recent years (Sih et al., 2004a,b; Sih & Bell, 2008; Dingemanse & Réale, 2005). At first glance, one might expect that individuals that show behavioural plasticity should have a selective advantage (Wilson, 1998; Dall, 2004), because they can adapt their behaviour to every situation and thus behave optimal in every context (Sih et al., 2004a,b). This makes it difficult to explain the behavioural inflexibility that is associated with animal personality. In addition, if behavioural differences have fitness consequences (Smith & Blumstein, 2008), then why do behavioural differences not converge into one optimal behavioural strategy over evolutionary time? Indeed, these inter-individual differences in behaviour are at times still presumed to be non-adaptive variation around what may be adaptive average (Dall et al., 2004). Yet, others argue that animal personalities can be given an adaptive explanation (Wolf et al., 2007; Wolf & Weissing, 2010).

Numerous studies have focused on explaining the emergence and maintenance of animal personalities from an evolutionary perspective (Dall et al., 2004; Wolf et al., 2007; Wolf et al., 2008; Schuett et al., 2010). It has been theorized that negative frequency dependent selection (Dall et al., 2004; Wolf et al., 2007; Wolf et al., 2008) can result in consistent inter-individual variation. More recently, it has been suggested that sexual selection may play a part in maintaining animal personalities (Schuett et al., 2010).

As postulated by Darwin, sexual selection arises from differences in reproductive success amongst individuals caused by competition over mates (Darwin, 1871). The anisogamy present in many species, two different genders with different gamete sizes, is believed to be at the base of gender differences in both behaviour and morphology (Andersson, 1994). Females usually produce fewer gametes but these are large and nutritious eggs, while males produce greater quantities of small, mobile sperm. The gender with the greatest investment into their gametes, and into parental care

when this is applicable, should be the most selective in their mate choice (Bateman, 1948). This results in two different phenomena; intersexual selection and intrasexual selection. Intersexual selection refers to mate choice, considering that females usually invest more in their offspring, this can often be seen as female mate choice. To maximize their fitness, females should select the best available male. Intrasexual selection refers to competition between individuals of the same sex, almost always males. This is why intrasexual selection is sometimes also referred to as male-male competition (Darwin, 1871; Andersson, 1994). Typically, these mechanisms lead to a greater variance in reproductive success of males in comparison to the variance in the reproductive success of females (Bateman, 1948).

Not many researchers have investigated sexual selection in the context of animal personalities (Schuett et al., 2010). This is surprising, as sexual selection is omnipresent in sexually reproducing species (Andersson, 1994), including those exhibiting animal personalities. In addition, sexual selection receives a lot of scientific attention in other contexts, illustrated by a search of the Web of Science (July 2012) that showed that 3.030 publications carried the term “natural selection” in their title, while 2.115 publications supported a title with the term “sexual selection”.

There must be inter-individual variation for sexual selection to take place; female choosiness cannot provide a selection advantage without variation between males. Considering that individual variation is one of the key aspects of animal personality, studying animal personality and sexual selection in conjunction could reveal interesting new insights. The aim of this thesis is to investigate the potential role of sexual selection, specifically female mate choice, in the emergence and maintenance of animal personality and to investigate how animal personality, in turn, might influence processes of sexual selection.

To investigate the dynamic between animal personality and sexual selection, this thesis is structured as followed. In the first chapter I will discuss examples of male variation in behaviour. In the following chapter I will investigate how female choosiness might emerge and how the presence of female choosiness might affect male variation in behaviour. In the third chapter I will address how variation in female preference might emergence. In the final chapter I will discuss how this variation in female preference might affect male variation in behaviour.

The relationship between animal personality and sexual selection is very complex. Animal personality may give rise to sexual selection, while at the same time sexual selection may contribute to the maintenance of animal personality. Unfortunately, many authors have only considered or examined one of these dimensions. In this thesis I will attempt to investigate both dimensions of the dynamic between sexual selection and animal personality.

Variation in male behaviour

For sexual selection to take place, females must obtain a selective advantage from being choosy. This is only possible if there is something to choose between, or put differently, when there is variation between males. Variation in behaviour is a defining feature of animal personality and this inter-individual variation in behaviour can be found in a range of taxa, including birds, lizards and fish. In this chapter I will discuss only a small, but representative subset of the many examples of male variation in behaviour.

In great tits, juvenile males demonstrate consistent inter-individual variation in exploration behaviour. Fast males explore a novel object or novel environment faster than slow explorers, but they also explore in superficial manner. Furthermore, fast males have more rigid habits and do not adjust as well to changes in the environment. In contrast, slow juvenile males approach novel objects or environments more cautiously, but also more carefully. Slow males also adjust better to changes in the environment (Verbeek et al., 1994). In a follow-up experiment it was found that fast explorers show higher levels of aggression than slower explorers. Verbeek et al. (1996) found that fast males started and won more fights than their slower counterparts. In other words, inter-individual variation in exploratory behaviour of males is correlated to inter-individual variation in aggressive behaviour.

Another species that shows variation in male behaviour is the side-blotched lizard. Males of this species exist in three different morphs, which are associated with great differences in behaviour. Males with an orange throat are aggressive and maintain a large territory with numerous females. Blue-throated males have territories of a smaller size and with fewer females than the orange males. However, blue males adopt a tireless mate-guarding tactic. Yellow males do not have a territory, but patrol on the outskirts of the territories of orange males. These males utilize a sneaker tactic; by appearing as a female, they try to achieve secretive copulations from females on the territories of the other males (Sinervo et al., 2000a; Bleay & Sinervo, 2007).

A particularly well-studied example of variation in male behaviour is the three-spined stickleback. Inter-individual variation in aggression (Huntingford, 1976), anti-predator tactics (Huntingford, 1987), nest-building (Rushbrook et al., 2008) and parental care (Stein & Bell, 2012) have been observed in male sticklebacks. In a ground-breaking study by Huntingford (1976), the response of male sticklebacks to territorial intruders was measured when the males were breeding and when they were not. The males that showed the highest level of aggression when breeding, were also the most aggressive outside the breeding season. Moreover, the level of aggression of the male individuals correlated positively with the boldness males demonstrated towards a predator. Therefore, Huntingford (1976) concluded that the aggressive response of male stickleback co-vary on several timescales and that male sticklebacks that demonstrate boldness towards predators are also more aggressive toward conspecifics.

More recently, Stein and Bell (2012) revealed that male sticklebacks also exhibit consistent individual differences in parental care across and within breeding clutches. In their study, males showed great inter-individual variation in parental behaviours, with some males spending most of

their time at the nest and other males spending considerably less time performing parental care. Those differences were maintained when reproducing a second time, with another female and in another environment, which is illustrated in figure 1. Considering that the individual differences were unrelated to male size or egg mass, it is unlikely that the differences reflect momentary differences in the males' condition (Stein & Bell, 2012). Not only do males differ in parental care, but they also vary in their nest building. Rushbrook et al. (2008) found a substantial degree of between male variation in both the structure and the size of nests built by male sticklebacks. In addition, when building nests sequentially males showed a considerable degree of repeatability. This finding is line with the suggestion that inter-individual variation between male sticklebacks is consistent over time (Rushbrook et al., 2008).

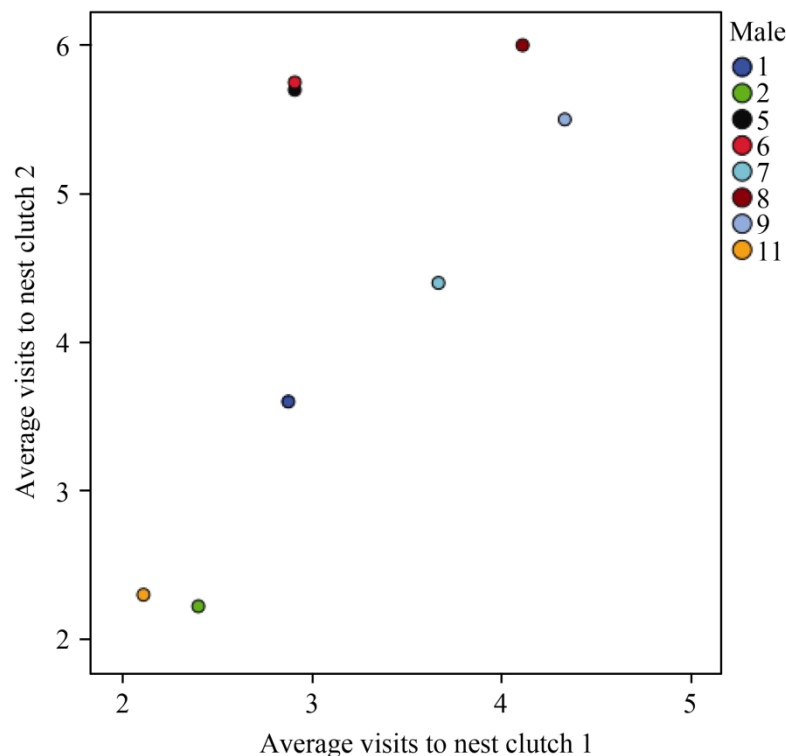


Figure 1: Consistency in the method of parental care of individual male sticklebacks. When the eggs of their first and second clutch were fertilized, the males were observed every day for 5 minutes during a ten day period. Each point indicates the average number of visits males made, in those 5 minutes during the ten day period, to their nest during their first and second clutch. ($r = 0.717$, $P = 0.045$, $n = 8$). It shows that when reproducing for a second time, in a different tank and with a different female, male sticklebacks retained their individual parenting style. (Stein & Bell, 2012)

As the examples above clearly demonstrate, consistent inter-individual variation in male behaviour is widely observed. This implicates that there is significant scope for females to be choosy and for sexual selection to take place. This lead to the question whether female preferences for certain male behavioural traits indeed evolved.

Emergence of female preference and its effect on male variation

The examples of the preceding chapter illustrate that variation in male behaviour can be found in several species; providing a clear opportunity for females to be choosy. But how might female choosiness emerge? In addition, if female choosiness is present, how might this influence male variation in behaviour? To determine this, I will take a closer look at the evolutionary mechanisms driving female choice. Subsequently, I will consider how female choice may promote specialisation.

Emergence of female preference

Several evolutionary mechanisms that may explain the existence of female choosiness have been put forward over the years. Females can benefit by being choosy either through direct or indirect benefits (Andersson & Simmons, 2006). Direct benefits refer to mostly material advantages, such as food, paternal care or shelter (Møller & Jennions, 2001). Indirect benefits are obtained by the female when the genetic fitness of her offspring is increased by selecting a certain male. This can occur through increased attractiveness of her sons, the sexy-son hypothesis (Fisher, 1930), or because all offspring is of superior genetic quality (Zahavi, 1975). Females can use so called indicator traits to determine whether a male is of good quality. These indicator traits must be honest signals of quality in order for a female preference to emerge. Sexual ornaments, like long tails and bright colours (Andersson, 1982; Godin & McDonough, 2003), have been recognized to be associated with heritable quality in a number of species. More recently, it has been postulated that personality traits might signal male quality as well (Schuett et al., 2010).

Effect of female preference on male variation

If male behaviours indicate quality, and quality is variable between males, females are expected to show a consistent preference for these behavioural traits. This would lead to a strong selection for these behavioural traits in males (Schuett et al., 2010). For a trait to be an honest signal of quality, it must be costly to produce (Zahavi & Zahavi, 1997). In principle, this should apply to behavioural traits that signal quality as much as it applies to morphological traits. Consequently, if males differ in quality, and a certain behavioural trait honestly signals this quality, there should be variation in this behaviour (Schuett et al., 2010). Thus, female choice may drive variation in male behaviour.

Indeed, there are several studies that indicate that male behaviour might signal quality. For instance, female Midas cichlid fish show a preference for more aggressive males, whereas males do not distinguish between females based on their aggression (Barlow, 1986). Aggression may be a signal of quality in male Midas cichlids, as pairs with an aggressive male are more successful in obtaining and maintaining a nesting site. Additionally, aggressive male Midas cichlids are better in safeguarding their offspring. Females show little variation in aggression or in parental care. (Barlow, 1986). Similarly, female fighting fish also prefer more aggressive males. Doutrelant and McGregor (2000) showed that after watching an antagonistic interaction between males, females favour winners over losers. As with Midas cichlids, males in this species have to safeguard their offspring (Jaroensutasinee & Jaroensutasinee, 2003). Perhaps, in both Midas cichlids and fighting

fish, the behavioural expression of aggression functions as an honest signal of parental quality (Schuett et al., 2010).

Not high, but low aggression in males is preferred by the females of the Japanese quail. In a study of Ophir and Galef (2003) females were able to observe antagonistic interactions between males, before selecting a male they had seen in the interaction. Females showed a greater preference towards the less aggressive males, as is illustrated in figure 2. This preference for less aggressive males remained significant when controlling for aggressive behaviour the males demonstrated towards the females during the agonistic interaction between the males. Furthermore, the preference of females for less aggressive males was only visible when females had observed the interactions.

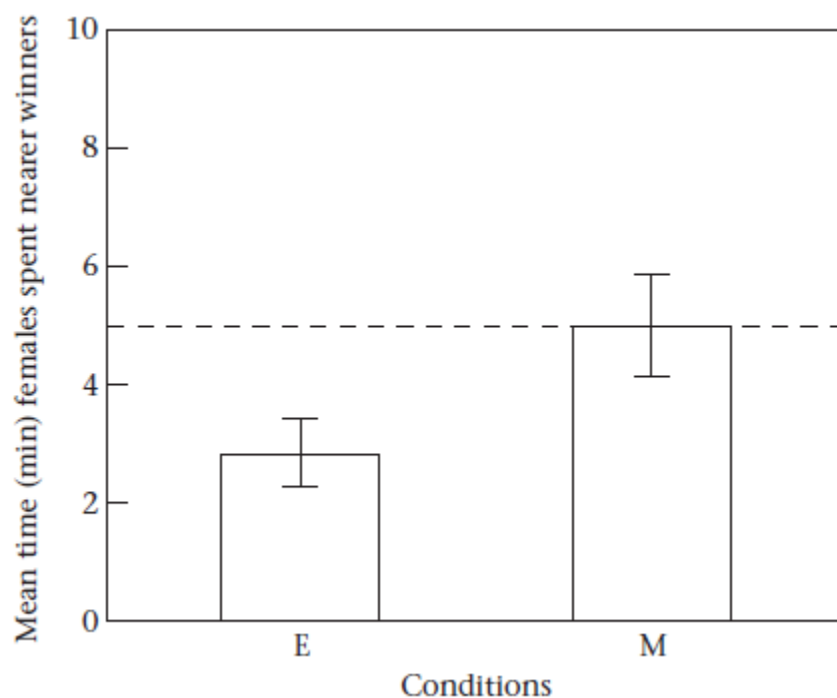


Figure 2. Female

preference for less aggressive males in Japanese quail. Mean time (minutes) \pm SE of females spent near the winners (i.e. more aggressive males). In the E condition females could observe the agonistic interaction between the males, in the M condition the females could not observe the agonistic interaction. Females in the E condition spent significantly more time near the loser than the winner (one-sample t-test: $t_{13}=3.92$, $p<0.01$). Females in the M condition showed no preference for either winners or losers. (one-sample t-test: $t_{14}=0.01$, $p<0.99$). (Ophir & Galef, 2003).

A positive correlation between aggression towards males and towards females was evident. The winners showed higher level of detrimental behaviour towards the females than the losers did (Ophir & Galef, 2003). It appears that females used what they observed in aggressive encounters between males to estimate which males might harass them more so that those males can be avoided. This would be a choice based on male consistency across context, with the females assuming that males that show high levels of aggression towards males would also demonstrate high levels of aggression towards females (Schuett et al., 2010). Interestingly, males of the Japanese quail do not perform parental care (Mills et al., 1997), in contrast to male cichlids and male fighting

fish. Therefore, high levels of aggression cannot function as an honest signal of parental quality in this species. This, in combination with the costs of mating with an aggressive male, may lead to a preference for non-aggressive males in Japanese quail (Schuett et al., 2010).

A final example indicating that male behaviour signals quality can be found in Trinidadian guppies. Individuals show variation in the level of risky predator inspection (Dugatkin & Alfieri, 1991). Female guppies show a preference for bolder males with more conspicuous colour patterns. Colour pattern and boldness are positively correlated in nature, but when colour pattern and behaviour were experimentally decoupled, female guppies still showed a preference for bolder males (Godin & Dugatkin, 1996). So, the behavioural trait boldness may be a signal of quality. This is underlined by the fact that bolder males have a higher chance to survive an interaction with a predator than males who show a lower level of boldness (Godin & Davis, 1995).

Arms race between males

Unanimous female preference may influence variation in male behaviour in a second manner. A strong female preference can result in an arms race between males, which then leads to males adopting different behavioural strategies. When a certain behavioural trait is desired, males will attempt to display the highest level of behavioural expression. However, if the behaviour is a (costly) honest signal, not all males may be able to display it (Schuett et al., 2010). As a consequence, males may resort to adopting different strategies. Indeed, Luttbeg (2004) argued that when females are able to correctly measure the quality of males, only high-quality males are expected to be selected as mates. Therefore, lower-quality males are very unlikely to be chosen as mates when they honestly indicate their quality. As a result, they may be better off changing to an alternative mating strategy that tries to avoid female choice. This way, female choice can lead to the emergence of alternative male mating behaviours, even when all females have the same preference. These alternative mating strategies can be seen in several species, including fish. In those species some males use a “courting” mating strategy, whereas other males exhibit a “sneaking” strategy. The courting males will invest in monopolizing resources like nests and territories, and the sneaker males will try to exploit the resources of the courting males and steal fertilizations (Taborsky 2001; Luttbeg, 2004) .

In summary, females may prefer certain behaviours, but some males are outcompeted in the arms race to display this behaviour. As a result, these males may gain more fitness by displaying another behaviour. So, arms race between males forces males of lower quality to opt for a different behavioural strategy, with consistent individual variation in male behaviour as a result.

Trade-off between adapting to natural selection or sexual selection

A last mechanism by which behavioural variation may arise, is when natural and sexual selection act in opposite directions. In this case, individuals face a trade-off between adapting to the two selective forces, which may promote the evolution of specialists with distinct behavioural traits. Hence, a trade-off between adapting to sexual selection or natural selection may play a role in maintaining male variation in behaviour.

A meta-analysis by Smith and Blumstein (2008) revealed evidence for a relationship between animal personality and fitness components. They found that bolder males had more reproductive

success than shy males, but shy males lived longer. Consequently, the overall fitness of shy males may not differ from bold males. In this example sexual selection seems to favour bold males, with bolder males demonstrating higher reproductive success, whereas natural selection seems to favour shy males. The fact that males with different behavioural expression of boldness have the same general fitness contributes to maintaining the inter-individual variation in boldness (Smith & Blumstein).

Another possible example of a trade-off between adapting to sexual selection or natural selection can be found in the side-blotched lizard. Sexual selection favours the orange-throated males, with the exception of when they increase too much in frequency, as their strategy can then be infiltrated by other morphs (Sinervo et al., 2000a). The eye-catching orange throat represents a badge of status (Smith, 1982) that indicates fighting ability and high aggression to other males and possibly high mate quality to females (Sinervo et al., 2000a). The difference in aggression and endurance between the orange males and blue males favours orange males in competitions. When the orange males exist at a low frequency, they are more successful in obtaining access to females than males with blue throats, which lose both territory and females to the orange males. However, orange-throated males have a lower survival rate than the blue and yellow males. So, orange males demonstrate a strategy that is favoured more by sexual selection, while the blue and yellow males exhibit a strategy that is favoured more by natural selection (Sinervo et al., 2000a). A trade-off between adapting to the two selective forces, may have led to this variation in male behaviour.

For a trade-off between adapting to natural or sexual selection to lead to variation in male behavioural tactics, individual differences in quality are not necessary. This is in contrast to the previous mechanism, where there is an arms race between males that differ in quality. When there is a trade-off, one behavioural strategy may be more successful in the context of sexual selection, whereas another behavioural strategy is more successful in the context of natural selection. Metaphorically speaking, animals that are of similar quality can go down a path favoured by natural selection or a path favoured by sexual selection. Which behavioural strategy is best is often dependent on negative frequency dependent selection (Sinervo et al., 2000a), resulting in the co-existence of two or more behavioural strategies.

In conclusion, female preference for male behavioural traits may lead to the evolutionary emergence and maintenance of male behavioural variation in several ways. First, assuming male behaviour is a costly indicator of quality, inter-individual variation in this behaviour is expected. This variation would consist of quantitative differences in behaviour, with males showing variation in a single behavioural trait. Second, a strong female preference can also stimulate an arms race between males, forcing some males of lower quality to opt for a different behavioural strategy altogether, because they are outcompeted by other males. In this case, qualitative behavioural differences are expected to arise. Third, a trade-off between adapting to sexual or natural selection may take place, with some male behavioural types being successful in the context of sexual selection, and others more successful in the context of natural selection, which can also lead to qualitative variation in male behaviour.

Emergence of variation in female preference

In the previous chapter I discussed that there is evidence of female preference for male behavioural traits, and that this preference can enhance behavioural variation between males. But, in the previous chapter I did not mention examples where females vary in their preference, which is something that can also be observed in animals. How can such variation in female preference emerge?

Emergence of variation in female preference

It has been hypothesized that mate choice enables females to select males that are more genetically compatible with their own genome (Tregenza & Wedell, 2000). Evidence supporting that some partners provide higher reproductive success than others can be found in a study done by Ryan and Altmann (Ryan & Altmann, 2001). They found that monogamous male mice achieved higher reproductive success when they were matched with their chosen female. Male mice that were paired with a female chosen by another male, or a female they did not prefer, achieved lower reproductive success. The benefits of compatibility between partners has been often discussed in the context of compatible immune systems (Alberts, 1993) and inbreeding avoidance (Bateson 1983). In this chapter I will focus on similar phenomena, but with an emphasis on behavioural compatibility.

Direct and indirect benefits

Males show variation in behaviour and, consequently, males can differ in their compatibility with females. This can lead to an emergence of variation in female preference. Selecting a male for compatibility can provide direct and indirect benefits. Direct benefits may be that certain pairs of personalities are better synchronized, resulting in better parental care. Indirect benefits may be that the progeny of similar or dissimilar pairs results in superior phenotype offspring.

Indeed, females may receive direct benefits from selecting a male that is more compatible with them in terms of behaviour. There is evidence indicating that behavioural coordination might lead higher reproductive success, due to better parental care. When pairs of cockatiels are behaviourally coordinated they perform better at incubation and achieve greater reproductive success than pairs of cockatiels that are not as behaviourally coordinated (Spoon et al., 2006). In addition, individuals from partnerships that demonstrate high behavioural coordination less often engage in extra-pair copulations than individuals from partnerships that demonstrate low behavioural coordination (Spoon et al., 2007).

Females may also benefit from preferring males with certain behaviour, because mating with a male exhibiting the behaviour results in superior phenotype offspring. For instance, in the side-blotched lizard the fitness of different behavioural types cycle like a rock-paper-scissors game. Males with orange throats are aggressive and have a large territory; this strategy is invaded by yellow sneaker males, which obtain secret copulations of females on the territory of the orange male. Blue males adopt a mate-guarding strategy, which invades the yellow 'sneaker' strategy. Finally, the aggressive strategy of the orange males invades the mate-guarding strategy of the blue

throated males (Sinervo & Lively, 1996). Because the fitness of the different behavioural strategies cycle in the fashion of a rock-paper-scissors game, the frequency of the behavioural types may provide a cue for mate choice (Sinervo & Zamudio, 2001). Sinervo and Zamudio (2001) also hypothesize that this may be valid for various other species with alternative mating strategies, like fish, as well as animals with population cycles, including mammals, where the stage of the population cycle can be determined by the density of the different behavioural types. Females should select partners that pass on superior genes to their offspring, but the genes that are desired is dependent upon the stage of the population cycle. In conclusion, females differ in their preference, because there is variation in the fitness of males, and that variation in fitness is maintained by frequency-dependent selection. The continuous presence of male variation results in maintenance of variation in female preference.

Assortative and disassortative mating

When females select partners that are more compatible, this can result in assortative or disassortative mating. It has been shown that great tits are more likely to be in a disassortative partnership (with regard to exploration behaviour) if the male tit is one year or older (Dingemanse et al., 2004). The researchers argued that disassortative partnerships between animals of extreme behavioural phenotypes could result in offspring with intermediate personalities, which may have fitness advantages. But, when disassortative mating is favoured by selection, because intermediate personalities have the highest fitness, one would expect that behavioural differences erode (Schuett, et al. 2010). However, Dingemanse et al (2004) also observed that selection pressures changed over the years, and these changes in selection pressures were in synchronization with differences in the environment. The changes in environmental condition, combined with fluctuating population density, may lead to these changes in selection pressures and thus maintain variation, even when disassortative mating takes place. In contrast, it is easier to imagine how assortative mating can maintain existing variation in behaviour, because individuals with dissimilar levels of behavioural expression will not mix (Schuett et al., 2010). Great tits that are in an assortative relationship have been shown to raise their young more successfully than great tits in a disassortative partnership. Fledglings reached a higher body mass when both parents were in an assortative partnership (with regard to exploration behaviour) (Both et al., 2005). However, Dingemanse et al. (2004) showed that great tits in an assortative relationship only performed better in years with high food availability. In poor years, the recruitment of offspring was not higher for assortative pairs.

In conclusion, females may vary in their preference, because males show variation in behaviour and, consequently, males differ in their compatibility with females. Selecting a male for compatibility may provide direct benefits if pairs of similar individuals are able to coordinate their behaviour better, or indirect benefits if the progeny of similar or dissimilar pairs is of superior phenotypic quality. Selecting a male based on compatibility can result in assortative or disassortative mating. With assortative mating, behavioural variation is maintained because individuals with dissimilar levels of behavioural expression will not form a partnership. Disassortative mating is expected to erode behavioural variation, but in the event of fluctuating selection pressures behavioural variation might still be maintained.

Variation in female preference

There are several examples when females show variation in female preference for a male behavioural trait. In zebra finches, females have been shown to exhibit consistent preferences for male behaviours, specifically song rate and aggression. Although individual females showed consistent preferences, they differed in the level of behavioural expression they preferred. Some females showed a preference for males with a high song rate, whereas other females showed a preference for males with a low song rate. Similarly, some females preferred aggressive males and other females preferred non-aggressive males (Forstmeier & Birkhead, 2004). Female zebra finches also differ in their preference for exploration behaviour. Females that are exploratory themselves prefer males that are exploratory as well. In contrast, females on the other side of the exploration spectrum show no preference for either males that are exploratory or non-exploratory (Schuett & Dall, 2009). Interestingly, the same holds true for male mate choice in great tits. Males selected for high exploration preferred females from the same selection line. On the other hand, males selected for low exploration showed no particular preference for exploration behaviour in females (Groothuis & Carere, 2005). Variation in female preference can also be found in the Trinidadian guppies. In general, female guppies prefer more conspicuous males with a noticeable colour pattern. However, female guppies differ in which male colour pattern they prefer, and consistently so (Godin & Dugatkin, 1995).

Both the female guppies and the female zebra finches showed consistency in their choice. Therefore, Schuett (2010) argued that it is unlikely that differences in female preference are caused by differences in evaluation abilities between the females. Instead, personality differences may play a role in determining female preferences.

Variation in female preference maintains variation in male behaviour

In the previous chapter I showed that variation in male behaviour may lead to the emergence of variation in female preference. But how does this variation in female preference in turn influence male variation in behaviour?

Variation in female preference might be one of the evolutionary mechanisms that maintains variation in male behaviour. Alonzo and Warner (2000) argued that variation in the female preference can explain the stable co-existence of male alternatives. They produced a theoretical model for a biological scenario where female choice depended on both male behaviour and the condition of the female. It was assumed that females vary in their fecundity and that males exist in a parental or non-parental form. Non-parental males did not perform parental care and were always available to the females. Parental males did perform parental care, but were not always available and finding those males required a cost in terms of energy expenditure. Female choice was dependent upon her own fecundity and the reproductive success of mating with either a parental or non-parental male. In the model, the variation in female fecundity led to variation in female preference. The model showed that this variation in preference can maintain different male alternatives even when there is no condition- or frequency-dependent fitness. (Alonzo & Warner, 2000).

An empirical example of this model can be found in the Mediterranean wrasse, where parental and non-parental males indeed coexist (Warner et al., 1991). Parental care is optional in this species and female choice depends on the reproductive success of mating with either type, the costs of finding them and the frequency in which both types of male occur in the population. Alonzo and Warner (2000) reasoned that this Mediterranean wrasse could be an example of when variation in female preference leads to the stable co-existence of two types of males. Furthermore, they claim that variation in female choice could explain the stable co-existence of male alternatives in other species as well.

In the side-blotched lizard, variation in male behaviour is also dependent on the condition of the female and her environment. Female side-blotched lizards show a great deal of variation in mate choice. Females of the species exist in two morphs. There are orange throated females that invest in quantity of offspring by producing many eggs and yellow throated females that invest in quality of offspring by producing large eggs. Therefore, orange females are favoured at low population density and yellow females are favoured at high population density (Sinervo et al., 2000b). Females of the side-blotched lizard select males based on their own phenotype, which is correlated with their genotype, and their current state. In a study by Bleay and Sinervo (2007) current state consisted of the number of clutches the female had laid. Before the females had laid any clutches, both the orange and yellow females demonstrated assortative mating. However, after females had laid their first clutch orange females preferred yellow males instead of orange males. In contrast, the yellow females still exhibited assortative mating, as can be seen in figure 3. Bleay and Sinervo (2007) argued that the vast amount of variation in female mate choice within the side-blotched lizard has the potential to maintain the genetic variation in males of the side-blotched lizard, despite the presence of divergent directional selection. One constant optimal behavioural strategy

does not exist in populations of the side-blotched lizard, so the best female mate choice is dependent upon the current environment. This can result in females changing in their preference to obtain the best males and several suitable male types may exist within the same population at any given time. They proposed that the number of ideal males should grow exponentially as a function of genotype•genotype•enviromental interactions to a magnitude where variation in both female preference and its reciprocal influence on male display traits are unlimited (Blay & Sinervo, 2007). In other words, when condition of the males and females vary, female choice depends on the present environment. Consequently, the interaction between the environment and the genotypes of the male and female may result in maintaining male variation in behaviour.

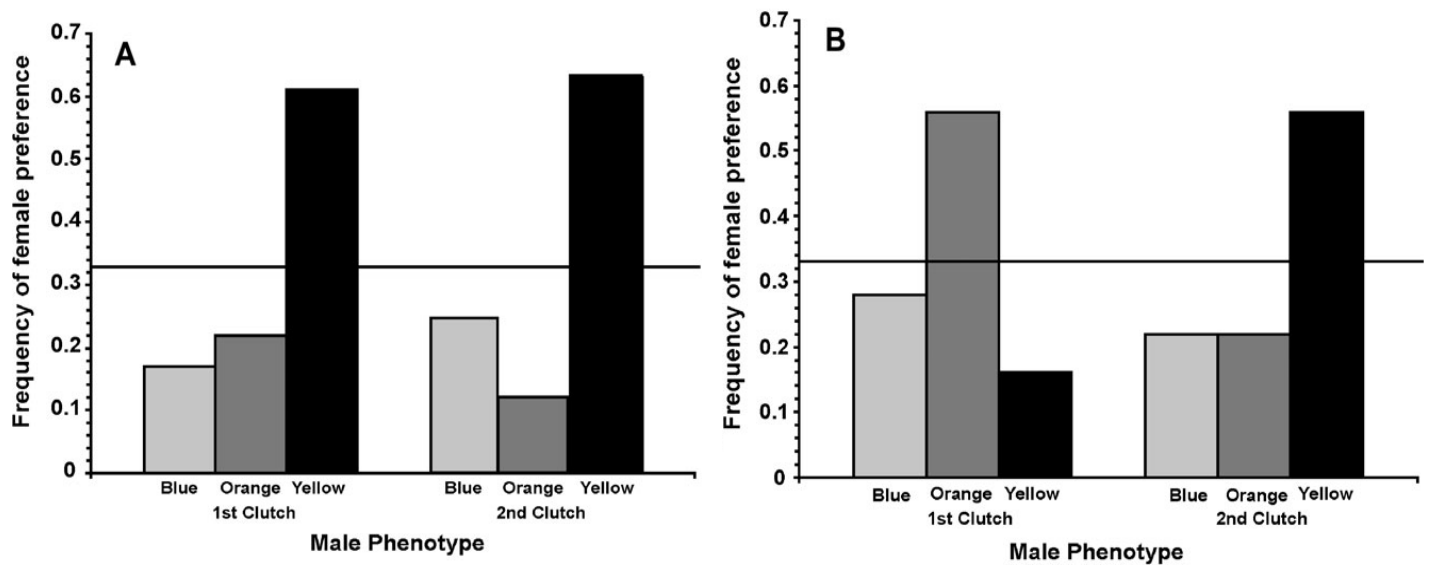


Figure 3 : Frequency of female preference for the male phenotypes. The black horizontal line shows the expected frequency of female preference when assuming a random probability of preference at 0.33. Figure 3(A) displays preference of the yellow females and figure 3(B) displays the preference of the orange females. Yellow females always show a preference for assortative mating, but orange females change to disassortative mating after the first clutch. (Bleay & Sinervo, 2007)

In conclusion, variation in female preference may be important in maintaining or even exaggerating variation in male behaviour. Female preference may depend on the current environment, her own condition and the condition of the male. The environment, frequency of certain male behavioural types, and condition of the females and males may vary and have reciprocal influences on each other. When those conditions are met, interaction between the state of the male and female and the current environment of the female may lead to maintenance of male variation in behaviour.

Conclusion & Discussion

The aim of this thesis was to investigate the potential role of sexual selection, specifically female mate choice, in the emergence and maintenance of animal personality and to investigate how animal personality, in turn, might influence processes of sexual selection.

Variation is a defining feature of animal personality and inter-individual variation in male behaviour can be found in a range of animals. This wide-spread variation implicates that there is scope for females to be choosy and sexual selection to take place.

If male behaviour honestly signals quality, and males show variation in behaviour, females can obtain evolutionary benefits from being choosy, resulting in the emergence of female preference. Female preference for male behavioural traits may lead to the evolutionary emergence and maintenance of male behavioural variation in several ways. First, if male behaviour is a costly indicator of quality, inter-individual variation in this behaviour is expected. This variation consists of quantitative differences in behaviour, with males showing variation in a single behavioural trait. Second, a strong female preference can also stimulate an arms race between males, forcing some males of lower quality to opt for a different behavioural strategy, because they are outcompeted by other males. In this instance qualitative differences in behaviour are expected. Third, a trade-off between adapting to sexual selection or natural selection may take place. Male strategies that more successful in the context of sexual selection, are less successful in the context of natural selection and vice versa, which can also lead to qualitative variation in male behaviour.

Males show variation in behaviour and therefore differ in their compatibility with females. This may lead to variation in female preference. Selecting a male for compatibility may provide direct benefits if pairs of similar individuals are able to coordinate their behaviour better, or indirect benefits if the progeny of similar or dissimilar pairs is of superior phenotypic quality. Selecting a male based on compatibility can result in assortative or disassortative mating. Assortative mating maintains behavioural variation, because individuals with dissimilar levels of behavioural expression will not form a partnership. Disassortative mating is expected to erode behavioural variation, but when selection pressures fluctuate behavioural variation might still be maintained. A number of studies have shown that female preferences are often variable (Godin & Dugatkin, 1995; Forstmeier & Birkhead, 2004). Nevertheless, individual females are often consistent in their preference, which may be a result of the personality of the female.

Variation in female preference may be important in maintaining or even exaggerating variation in male behaviour. This is assuming female preference depends on her current environment, her own condition and the condition of the male. It is further required that both the environment, frequency of certain male behavioural types, and condition of the females and males vary and have reciprocal influences on each other. In this instance, interaction between condition of the male and female and the current environment of the female may lead to maintenance of male variation in behaviour.

In conclusion, female mate choice may influence the emergence and maintenance of animal personality in several ways. The existence of female preference can lead to the emergence of quantitative and qualitative male variation in behaviour. Additionally, when there is variation in female preference this may maintain or even enhance variation in male behavioural traits.

Considering that inter-individual variation is a defining characteristic of animal personality, female mate choice may play an important role in the emergence and maintenance of animal personality. Therefore, when studying animal personality it should be considered whether (and, if so, how) sexual selection plays a part in generating behavioural variation. Not only does female mate choice influence animal personality, but animal personality also affects processes of sexual selection. In many cases where variation in female preference is present, individual females are consistent in their choice. This indicates that personality differences between females (partly) determine female mate choice. Animal personality may therefore have a significant effect on the evolutionary dynamics and outcomes of sexual selection. Consequently, when studying intersexual selection, personality differences, both in females and males, should be taken into account where relevant.

The focus of this thesis was mostly on intersexual selection, but intrasexual selection might also influence animal personality. Unfortunately, it is often difficult to separate the two forms of sexual selection. For instance, when there is an arms race between males there are probably components of both forms of sexual selection present. But, considering that intrasexual selection can lead to variation in male behaviour (Taborsky, 1994; Gross, 1996; Hurtado-Gonzales & Uy, 2010), it is important to take into account if and how intrasexual selection may contribute to inter-individual variation when studying animal personality.

In this thesis I primarily discussed female mate choice, but male mate choice may also influence the emergence and maintenance of animal personality. For instance, male great tits show variation in their preference for exploratory females in a very similar way to how female zebra finches show variation in their preference for exploratory males. One might also ask how mutual mate choice may influence the evolution of animal personality. For example, if mutual mate choice leads to assortative mating this could contribute to maintaining behavioural variation within populations. Therefore, in future studies the preference of both sexes should be considered.

I focused mainly on inter-individual variation in this thesis, and I did not explicitly examine another defining feature of animal personality; consistency over time and across contexts. It will only provide females with evolutionary benefits if males continue to exhibit the behaviour they were chosen for. For that reason, consistency over time is of great importance when females are selecting males based upon their behaviour. Additionally, consistency might also provide an opportunity for sexual selection, if it provides females with benefits to choose a male that behaves predictably across contexts. For example, it was discussed that in Midas cichlids and fighting fish high levels of aggression might signal high levels of parental care. This illustrates that consistency across contexts in males might provide females with benefits, because females can use one behaviour to estimate the expression of another behavioural trait in the males they are evaluating. So, in addition to variation, which provides scope for the selecting sex to obtain evolutionary benefits from being choosy, consistency may also be of consequence for sexual selection. Animal personality is therefore, in all its aspects, of importance for processes of sexual selection.

References

- Alberts, S.C., Ober, C. (1993) Genetic variability of the MHC: a review of non-pathogen-mediated selective mechanisms. *American Journal of Physical Anthropology*, 36: 71–89
- Alonzo, S.H., Warner, R.R. (2000). Female choice, conflict between the sexes and the evolution of male alternative reproductive behaviours. *Evolutionary Ecology Research*, 2: 149–170
- Andersson, M. (1982) Female choice selects for extreme tail length in a widowbird. *Nature*, 299: 818–820.
- Andersson, M. (1994). *Sexual selection*. Princeton, New Jersey: Princeton University Press.
- Andersson, M., Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in Ecology & Evolution*, 21 (6): 296–302.
- Barlow, G.W. (1986). Mate choice in the monogamous and polychromatic Midas cichlid, *Cichlasoma citrinellum*. *Journal of Fish Biology*, 29 (Issue supplement SA): 123–133.
- Bateman, A.J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, 2: 349–368.
- Bateson, P. (1983). Optimal outbreeding. In Bateson, P. (Ed), *Mate choice*. (pp. 257–277). Cambridge, U.K.: Cambridge University Press.
- Bleay, C., Sinervo, B. (2007). Discrete genetic variation in mate choice and a condition-dependent preference function in the side-blotched lizard: implications for the formation and maintenance of coadapted gene complexes. *Behavioural Ecology*, 18 (2): 304–310.
- Boissy, A. (1995). Fear and fearfulness in animals. *The Quarterly Review of Biology*, 70 (2): 165–191.
- Both, C., Dingemanse, N. J., Drent, P. J., Tinbergen, J.M. (2005). Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, 74: 667–674.
- Carere, C., Drent, P.J., Privitera, L., Koolhaas, J.M., Groothuis, T.G.G. (2005). Personalities in great tits (*Parus major*): stability and consistency. *Animal Behaviour*, 70: 795–805.
- Dall, S.R.X., Houston, A.I., McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7: 734–739.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: Murray.
- Dingemanse, N.J., Both, C., Drent, P.J., van Oers, K., van Noordwijk, A.J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64 (6): 929–938.
- Dingemanse, N.J., Both, C., Drent, P.J. & Tinbergen, J.M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B: Biological Sciences*, 271: 847–852.
- Dingemanse, N. J. Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142: 1165–1190.
- Doutrelant, C., McGregor, P.K. (2000). Eavesdropping and mate choice in female fighting fish. *Behaviour*, 137 (12): 1655–1669.
- Dugatkin, L.A., Alfieri, M. (1991). Tit-for-tat in guppies (*Poecilia reticulata*): the relative nature of cooperation and defection during predator inspection. *Evolutionary Ecology*, 5 (3): 300–309.
- Fisher, R.A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Forstmeier, W., Birkhead, T.R. (2004). Repeatability of mate choice in the zebra finch: consistency within and between females. *Animal Behaviour*, 68 (5): 1017–1028.

- Godin, J.J., Davis, S.A. (1995). Who dares, benefits: predator approach behavior in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society B: Biological Sciences*, 259: 193–200.
- Godin J.J., Dugatkin, L.A. (1995). Variability and repeatability of female mating preference in the guppy. *Animal Behaviour*, 49 (6): 1427–1433.
- Godin J.J., Dugatkin, L.A. (1996). Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences*, 93 (19): 10262–10267.
- Godin, J.J., McDonough, H.E. (2003). Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral Ecology*, 14 (2): 194–200.
- Gosling, S.D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127 (1): 45–86.
- Groothuis, T.G.G., Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, 29 (1): 137–150.
- Gross, M.R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution*, 11 (2): 92–98.
- Huntingford, F.A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, 24 (2): 245–260.
- Hurtado-Gonzales, J.L., Uy, J.A.C. (2010) Intrasexual competition facilitates the evolution of alternative mating strategies in a colour polymorphic fish. *BMC Evolutionary Biology*, 10 (391): 1–11.
- Jaroensutasinee, M., Jaroensutasinee, K. (2003). Type of intruder and reproductive phase influence male territorial defence in wild-caught Siamese fighting fish. *Behavioural Processes*, 64 (1): 23–29.
- Koolhaas, J.M., Korte, S.M., de Boer, S.F., van der Vegt, B.J., van Reenen, C.G., Hopster, H., de Jong, I.C., Ruis, M.A.W., Blokhuis, H.J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, 23: 925–935.
- Luttbeg, B. (2004). Female mate assessment and choice behavior affect the frequency of alternative male mating tactics. *Behavioral Ecology*, 15 (2): 239–247.
- Mills, A.D., Crawford, L.L., Domjan, M., Faure, J.M. (1997). The behavior of the Japanese or domestic quail *Coturnix japonica*. *Neuroscience and Biobehavioral Reviews*, 21 (3): 261–281.
- Møller, A.P., Jennions, M.D. (2001). How important are direct fitness benefits of sexual selection? *Naturwissenschaften*, 88 (10): 401–415.
- Ophir, A.G., Galef, B.G. (2003). Female Japanese quail that ‘eavesdrop’ on fighting males prefer losers to winners. *Animal Behaviour*, 66 (2): 399–407.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J. (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82 (2): 291–318.
- Ryan, K.K., Altmann, J. (2001). Selection for male choice based primarily on mate compatibility in the oldfield mouse, *Peromyscus polionotus rhoadsi*. *Behavioral Ecology and Sociobiology*, 50 (5): 436–440.
- Rushbrook, B.J., Dingemanse, N.J., Barber, I. (2008) Repeatability in nest construction by male three-spined sticklebacks. *Animal Behaviour*, 75 (2): 547–553.
- Schuett, W., Dall, S.R.X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77 (5): 1041–1050.
- Schuett, W., Tregenza, T., Dall, S.R.X. (2010). Sexual selection and animal personality. *Biological Reviews*, 85 (2): 217–246.

- Sih, A., Bell, A.M., Johnson, J.C. (2004a). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19 (7): 372-378.
- Sih, A., Bell, A.M., Johnson, J.C., Ziemba, R.E. (2004b). Behavioural syndromes: an integrative overview. *The Quarterly Review of Biology*, 79 (3): 241-277.
- Sih, A., Bell, A.M. (2008). Insights for Behavioral Ecology from Behavioral Syndromes. *Advances in the Study of Behavior*, 38: 227-281.
- Sinervo, B., Lively, C.M. (1996) Rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380: 240-243.
- Sinervo, B., Miles, D.B., Frankino, W.A., Klukowski, M., DeNardo, D.F. (2000a). Testosterone, endurance, and Darwinian fitness: natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards. *Hormones and Behavior*, 38 (4): 222-233.
- Sinervo, B., Svensson, E., Comendant, T. (2000b) Density cycles and an offspring quantity and quality game driven by natural selection. *Nature*, 406: 985-988.
- Sinervo, B., Zamudio, K.R. (2001). The Evolution of Alternative Reproductive Strategies: Fitness Differential, Heritability, and Genetic Correlation Between the Sexes. *Oxford Journals*, 92 (2): 198-205.
- Smith, M.J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Smith, B.R., Blumstein, D.T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19 (2): 448-455.
- Spoon, T.R., Millam, J.R., Owings, D.H. (2006). The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour*, 71 (2): 315-326.
- Spoon, T.R., Millam, J.R., Owings, D.H. (2007). Behavioural compatibility, extrapair copulation and mate switching in a socially monogamous parrot. *Animal Behaviour*, 73: 815-824.
- Stamps, J.A., Groothuis, T.G.G. (2010). Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365: 4029-4041.
- Stein, L.R., Bell, A.M. (2012). Consistent individual differences in fathering in threespined stickleback *Gasterosteus aculeatus*. *Current Zoology*, 58 (1): 45-52.
- Taborsky, M. (1994). Sneakers, Satellites, and Helpers: Parasitic and Cooperative Behavior in Fish Reproduction. *Advances in the Study of Behavior*, 23: 1-100
- Taborsky, M. (2001). The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *Journal of Heredity*, 92 :100-110.
- Tregenza, T., Wedell, N. (2000). Genetic compatibility, mate choice and patterns of parentage: Invited review. *Molecular Ecology*, 9 (8): 1013-1027.
- Verbeek, M.E.M., Drent, P.J., Wiepkema, P.R. (1994). Consistent differences in early exploratory behaviour of male great tits. *Animal Behaviour*, 48 (5): 1113-1121.
- Verbeek, M.E.M., Boon, A., Drent, P.J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, 133 (11-12): 945-963.
- Warner, R.R., Wernerus, F., Lejeune, P., van den Berghe, E. (1991). Dynamics of female choice for parental care in a fish species where care is facultative. *Behavioural Ecology*, 6 (1): 73-81.

Wilson, D. S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society B: Biological Science*, 353 (366): 199–205.

Wolf, M., van Doorn, G.S, Leimar, O., Weissing, F.J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447: 581–584.

Wolf, M., van Doorn, G.S., Weissing, F.J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, 105 (41): 15825–15830.

Wolf, M., Weissing, F.J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Science*, 365: 3959–3968.

Zahavi, A. (1975). Mate selection : selection for a handicap. *Journal of Theoretical Biology*, 53 (1): 205–214.

Zahavi, A., Zahavi, A. (1997). *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. New York: Oxford University Press.