Can animal personality speed up speciation?

One of the most intriguing parts about the study of biology is the incredible biodiversity on our planet. The question where life originated and how it branched out into the many different forms that shape nature today is one that has been on the human mind for ages. Perhaps the most well-known biological work of all time, *'The Origin of Species'* by Charles Darwin, put the theory of evolution into an entirely new spotlight when it was published in 1859, although it wasn't until early into the twentieth century with the works of most notably Fisher (Fisher et al, 1930) that evolutionary biology became a well-established branch in biological studies. Since then, in the last century and especially the last few decades, the technology for genetic research has surged, and with it the understanding of many evolutionary processes (Appels et al, 2014), and with it came an increased understanding and focus on certain evolutionary processes, like speciation (Rice et al, 1993)(Gavrilets, 2014).

Speciation is the process where two individuals originally of the same species have genetically diverged so far from each other that they can no longer reproduce together, and can therefore no longer be considered as the same species (Encyclopaedia Britannica). Because this happens on a timespan covering between tens to even thousands of generations, speciation is a very difficult topic to study (Noor et al, 2006). Aside from that, the dynamics influencing speciation (habitat selection, sexual selection, mutations, etcetera) Often work at the same time and both with and against each other, making it hard to determine confounding factors in speciation research. One of the dynamics that could potentially influence the process of speciation, but has been relatively understudied, is animal personality. Animal personality or behavioural correlation across situations is defined as the tendency for individuals to differ consistently across situations. These tendencies also stay stable over time. (Sih et al., 2004). Per definition this already shows promise for speciation, as two individuals with different personalities will interact differently with both their physical and social environment, and can make different choices in for example habitat and mates, which can result in non-random gene flow and ultimately contribute to speciation. I will go into further detail on this interaction, as so far there has been limited evidence describing a direct correlation between animal personality and speciation.

Models of speciation

For speciation to happen, certain requirements have to be met: there should be some form of genetic variation between or within subpopulations of a species and limited gene flow between these different genotypes (Via, 2009). Genetic variation is usually already present in most healthy populations and is caused by random mutations. In separated populations, local adaptations to different habitats will cause further diverging of genotypes. Mutations happen gradually over time and at random, and in a healthy population size with random mating will almost certainly not lead to speciation via genetic drift in a timespan that allows for any realistic studies. Take for example the human genome, where it is estimated that per generation one mutation per 30 million base pairs takes place (Xue et al., 2009). On top of that, most single base pair mutations don't cause any significant differences in phenotype. For mutations or adaptations to persist and add up to actual significant genotypic differences, limitations to gene flow are essential.

One mechanism that can lead to genetic divergence among groups originating from the same population is reproductive isolation. Isolation can be caused by external factors, like a habitat splitting up due to natural disasters (Corl et al, 2012) or human interference (Paris et al, 2015). When two parts of a previously unified population become separated and genetically diverge over time, this is known as the classic allopatric model. Allopatry has for a long time been the best described

and well accepted condition for speciation, most notably thanks to Ernst Mayr and his work Systematics and the Origin of Species. In the threshold model of reproductive isolation, it was hypothesised that diversity is dependent of both spatial and genetic distance between two subpopulations, creating an exponential growth model that allows for a rapid increase in diversity after spatial and genetic distance passed a certain 'threshold', reminiscent of the sudden increase in a graph of an exponential function (Gavrilets et al, 1998, 2014). However, a physical barrier between individuals is not always needed for spatial isolation. Animals (or genotypes) often choose to disperse from their original populations to settle elsewhere. This can be due to a number of reasons, like deteriorating habitat quality, increasing competition over resources or avoidance of inbreeding (Hamilton & May, 1977). If the dispersing individuals were to be a random sample of the population, then this process likely wouldn't lead to speciation, as the dispersing population would contain roughly the same genetic composition as the natal population, and a random gene flow would be sustained by new individuals leaving the natal population at random. However, this is often not the case. Both likelihood of dispersing and direction of dispersal are correlated with phenotype and vary within populations (Colbert et al, 2009)(Myers and Krebs, 1971). This leads to similar phenotypes being more likely to disperse and ending up in a new habitat together, instead of being a random sample of the natal population. This can also be described as directed gene flow. Not only that, but after the individual makes the decision of leaving its natal habitat, it has to make a second decision on where to settle for its new territory. This is once again not a random process, as an individual will try to find a territory that best matches his own phenotype, which further increases the chance of individuals with similar phenotypes ending up in a habitat together (Jacob et al, 2015).

Even within populations, habitats are often heterogenous and instead of migrating, individuals can choose habitats within the population that fit their phenotypes best, i.e. they choose habitats where they are expected to maximise their fitness (Dreiss et al, 2011). This adaptive habitat choice is also known as matching habitat choice (Edelaar et al 2008, 2012) For example, individuals may select their habitat based on their food preference, or the ability to be locally camouflaged (Bibiana Rojas, 2016). While there are cases where it's not entirely clear whether or not matching habitat choice is actually an active choice by the animal based on its phenotype, or just a product of selection or phenotypical adaptation, there is evidence that experimentally altering phenotypes influences habitat choice (Karpestam et al, 2012). There is also evidence that individuals with a less competitive phenotype inhabit lower quality habitats without even trying to compete for higher quality habitats, as smaller male cichlids showed a tendency to settle for lower quality habitats, even when no larger males were present during the decision. (Taborsky et al, 2014), indicating that while the results would likely be the same if smaller phenotypes did try to compete, animals can make the conscious decision to match their habitat according to their chance of competing for it. So, in a heterogeneous habitat with a considerable size, inhabitants of different microhabitats might never meet, even when there is no physical barrier between them. This is the sympatric model for speciation, and up until relatively recently the idea that any significant speciation could occur without spatial restrictions to the gene flow has been very controversial and often dismissed (Gavrilets, 2014). Another behavioural aspect that factors into the sympatric speciation model is assortative mating. Sexual selection is already known to be a very strong factor in the process of evolution and speciation (Brooks et al, 2001). It makes sense that a selection pressure so closely related to reproduction is such a strong influence on the directions of gene flow. Concepts like Fisherian runaway and sexual conflict of reproduction can account for rapid changes within a population over just a few generations. Assortative mating is the tendency for an individual to prefer mating with an individual that shares phenotypical traits with them. This is particularly interesting for speciation because for assortative mating to happen, an innate variation already has to be present in the form of different phenotypes to choose from, which can further be cemented by individuals looking for similar traits to

themselves. There is evidence that even a first generation hybrid of two phenotypes will already have a strong preference to other individuals of the hybrid phenotype over the two phenotypes of its parents, creating the possibility of an entirely new subpopulation with assortative mating in the span of one generation (Selz et al, 2013).

Can animal personality facilitate speciation?
Now that some of the precursory dynamics leading to speciation have been outlined, we can look for situations where animal personality could in theory facilitate these processes, and look for evidence in current evolutionary studies in nature that could support these theories being true in practice.

Personality dependent dispersal:
As has been told before, dispersal is usually not a random process, and is dependent on certain phenotypical traits. This can be in the form of morphological differences, since migration is quite a costly procedure in terms of energy because of travel costs, predation risk and possible competition for space or resources in the new habitat. Aside from that, there is also the risk of dispersing but not finding a new suitable habitat. All of this means that only individuals that are in well enough shape to afford the short term disadvantages of dispersing can afford to do so. This usually equates to greater body size or, depending on the species, larger wing span or higher body fat percentage (Murren et al, 2001). However, recent studies have shown that there is also a behavioural correlation with dispersal. (Cote et al, 2010). Individuals that disperse to new locations are generally significantly more active, bold and aggressive than individuals who stay resident, not only directly before and after dispersal, which is to be expected and could be counted as behavioural plasticity, but consistently throughout their entire life in some studied cases.
By far the most studied behavioural trait in correlation with dispersal is exploration in a novel environment (Wey et al, 2015). Activity, exploration and boldness were linked to a reduced dispersal latency and an increased distance of dispersal and exploration in novel habitats. More importantly, in several studies of dispersal in mice, these differences were shown to be both consistent within an individual's lifespan (Myers & Krebs 1971) and consistent between parent and child (Krackow 2003), indicating that that the traits are heritable to a degree, which is very important to make an argument for speciation. It should be noted that these results were not derived from the same studies, so caution should be exercised when drawing conclusions about the combination of consistency and heritability. On top of that, while the study by Myers & Krebs does show consistent behavioural differences between dispersers and residents, their study does not cover the difference in boldness or exploration behaviour pre dispersal in relation to the likelihood of dispersal. Furthermore, the study results show that dispersers are actually less exploring than residents, which would go against the idea that bold individuals have a tendency to disperse sooner than shy individuals. However, in the context of an entirely new environment, it makes sense that recently dispersed individuals are more careful about exploring than individuals who stay in a known environment.
For aggressiveness, the differences between dispersing and resident individuals are less clear cut. There are two ways in which aggression can influence the dispersal of certain individuals. The first scenario is that passive individuals get forced to leave the population because they cannot compete for resources with the more aggressive individuals (Brandt, 1992). In other cases the aggressive individuals are actually the ones with a higher tendency to disperse because of their advantage in competing for new territory. (Cote et al, 2010). While these two occurrences are directly

contradictory to each other, they can actually both exist within the same species (Cant et al, 2001). It is often not clear which one of the two will happen, and it is likely dependant on other factors such as quality of habitat, average age and sexual distribution of the population. As with boldness, aggression also has an effect on both the pre and the post dispersal period, depending on the other populations surrounding the resident habitat. If a dispersing individual ends up in an already occupied habitat as opposed to an empty one, both low aggression and high aggression can provide advantages for the immigrant depending on the levels of aggressiveness of the resident population. If the resident population is very aggressive, being aggressive yourself as an immigrant will lead to increased conflict and the possibility of getting wounded, which is very costly. Therefore it can be more advantageous to be more submissive to higher your chances of getting accepted into the resident population. Alternatively, if the resident population is very submissive, being aggressive yourself is advantageous because you have a greater chance at competing for resources with a much lesser risk of conflict and getting wounded. Because the relation between aggression and dispersal is heavily influenced by factors from outside, it is much harder to study and make predictions for. Therefore, it is difficult to find studies that examine the relation between aggression and dispersal in a controlled manner.

One of the aspects of animal personality that has not been explored much in relation to dispersal is sociability (Cote et al, 2010). In the classic social cohesion hypothesis (Bekoff, 1977) the theory is that individuals who are social with others are less likely to disperse. It makes sense to suggest an animal has less reason to disperse if it has social ties within the population, similar to how humans don't like to leave family and friends. While there are studies that show individuals that show less social behaviour are more likely to disperse, they do not show how sociability as a personality trait relates to dispersal. Another problem with using sociability as a measurement is that it is often closely related to aggression, since aggressive individuals tend to be less social as well. It is therefore hard to distinguish which one of the two is a confounding factor. A study that did find a connection between early life sociability and dispersal in a later stage of life in common lizards (Cote & Clobert 2007) showed that the relation between dispersal and sociability is dependent on population density. Social individuals were shown to be more likely to disperse when population densities got low, while asocial individuals dispersed more often when the population density increased.

Personality dependent habitat choice
Because habitats are often heterogeneous, animals have the liberty to maximize their fitness by avoiding competition over certain resources and picking a habitat that is most optimal for their phenotype by occupying a specific niche within a habitat. This choice can be made based on a preference for a certain food, nesting sites or inconspicuousness. Another word for this is resource polymorphism, and it's quite prevalent in many different species (Smith et al, 1996). While niche formation is usually less obvious and defined within species than between different species occupying the same habitat, it can be observed (Cloyed & Eason 2017). Foraging behaviour is one of the prime differences observed between individuals of the same species. Parameters like distance travelled during foraging, Tendency to forage in groups or alone and differences in hunting strategies, for example sitting and waiting for prey or actively chasing prey yourself, have shown to be variable within many species. While this was long thought to be an example of phenotypic plasticity, recent studies have shown that these strategies often stay consistent over time and can be tied to differences in personality traits like boldness, sociability and activity (Toscano et al, 2016). In theory, these differences in foraging strategies should have a considerable influence on habitat choice. An individual with a sit and wait hunting strategy can increase its success by having a habitat with sufficient cover and camouflage, while an active hunter might be more inclined to have a larger and more open territory to cover more ground while foraging. Aside from method of foraging, food

preferences can also differ within species (Dix et al., 1968)(Robb et al, 2016), although it is often disputable whether the correlation between diet and habitat is a choice of habitat based on food preference or an adaptation in diet based on the environment, and most evidence seems to point towards the latter case. Another way in which personality differences can affect habitat choice is a less severe version of migration based on sociability. In many species, more social individuals will huddle up together near the centre of the territory, while less sociable individuals will spread out towards the outskirts (Lill, 1968). Sometimes this is a case of conscious avoidance of their conspecifics based on sociability, and in some cases it is a result of less aggressive individuals being pushed towards the outskirts of the habitat due to losing fights against more aggressive individuals and subsequently avoiding them.

Personality dependent sexual preference

As stated before, sexual selection is one of the strongest selection pressures on gene flow. Individuals will often have a preference for partners who show phenotypical traits similar to their own, also known as assortative mating (Keats & Sherman 2013). Usually when referring to 'similar phenotypical traits', the focus is on the morphology of the animal, however there is evidence that sexual selection also plays a part in creating and maintaining animal personalities (Schuett et al, 2010). Therefore, it could be worthwhile to further research personality traits in their role in mate selection and reproduction and see if assortative mating can happen based on personality.

Aside from general behaviour, mating behaviour might also be influenced by animal personality. There is a wide variety of animals that have certain mating behaviour to seduce potential partners to mate with them over others. In some species, there are different options for mating behaviour, with different females having preferences for different types of behaviour (Sinervo & Lively, 1996). When an individual consistently uses the same mating strategy through its life history, this could be seen as a form of animal personality, and therefore be of interest for the research question. Even though in most cases these kind of systems keep diversity in stand, losing one of the morphs for whatever reason can result in rapid phenotypic diversification between populations (Corl et al, 2010).

Evidence

The previous section outlines how **in theory** it's very reasonable for animal personality to influence the process of speciation, but the fact of the matter is that there is currently very little hard evidence showing the direct correlation. Many studies in which animal personality could play a role don't specifically look for it, and even when animal personalities get considered as a factor it's often not clear to what extent. Below I will list several pieces of evidence both arguing for and questioning the influence of animal personality on the speciation process.

Dispersal and habitat choice

In terms of dispersal habitat choices, there is quite some evidence that *might* suggest a correlation between type of habitat and personality traits, but it is often unclear which is the cause and which is the effect. For example, a study has shown that blue tits show strong differences in handling aggression, exploration and nest defence between inhabitants of an evergreen forest and a deciduous forest (Dubuc-Messier et al, 2016), with deciduous inhabitants showing significantly higher handling aggression and exploration speed than their evergreen counterparts. One implication could be that aggressive, high activity individuals migrate away from the evergreen population and settle in deciduous habitats because they have a preference for it. However, this does not appear to be the case. The differences in behaviour between the populations appear to be in line with a recent expansion of the pace-of-life syndrome hypothesis (Ricklefs & Wikelski, 2002)(Réale et al, 2010). The original hypothesis states that populations of the same species can develop a difference in certain life history traits according to whether they live in a slow or a fast pace of life environment. For example,

birds who live in a slow pace of life environment will live longer and lay smaller clutches than birds in a fast pace of life environment. The study by Réale in 2010 states that personality is closely linked to these traits and should be included in the hypothesis. The blue tit study shows that the traits of their subject populations follow this hypothesis, with the deciduous habitat being a fast pace of life environment and the evergreen habitat a slow pace of life environment. Aggression and high exploration are classic signs of a fast pace of life population. Therefore, in this case it is the environment dictating the personality, and not the other way around.

In a study on a species of desert fish, differences in boldness between subpopulations was also proven to be an adaptation under selection pressure (Moran et al, 2016), most notably to the differences in predation risk between populations. This study makes an even stronger case for environment being the cause, since fish are unable to travel between the desert lakes, leaving out the possibility of habitat choice based on personality.

Another study shows that personality types are heavily influenced by early life environmental conditions in jumping spiders (Liedtke et al, 2015). Spiders raised in an environment deprived of social or physical stimuli showed less exploratory behaviour throughout their lives than spiders raised in either a socially or a physically enriched environment. With evidence like this, one could assume that personality is not an important factor for genetic divergence between habitats, and instead is just a confounding result with the same cause. However, in recent years more and more evidence has shown up for the personality-matching hypothesis. For example, a recent study on dunnock birds shows that bolder individuals are more likely to settle in an environment with high human disturbance, while shy individuals tend to stay away from these (Holtmann et al, 2017). Even though there is an influence from phenotypical plasticity here due to birds getting bolder with age, it's not nearly as strong as the innate differences in boldness between individuals. It should be noted, however, especially when compared to the previous examples, that no tests were taken to check for early environmental influences from human disturbance on an individuals boldness. But regardless of the origin of the differing personality traits, an influence on habitat choice can be proven.

A study on brown bears shows that consistent differences on habitat selection based on personality exist between individuals (Leclerc et al, 2016). GPS data gathered over 6 years shows that individual bears deviated from the population-scale habitat preference of a cut-wood habitat over a bog habitat, and that the preferences of an individual bear stayed consistent over time. While the underlying reason for these preferences is unknown (once again, early life exposure to a certain type of habitat could cause the development of the preference), the preference can be interpreted as a form of personality, and the results suggest that it may be at least partly heritable.

Sexual selection/Hybridization

In terms of sexual selection, evidence for influence by personality traits is easier to test for in a controlled environment, and has therefore also brought more results over the past few years. There are examples for multiple aspects of personality that play a role in the sexual selection progress. A very promising piece of evidence, especially in the context of speciation, is a study that shows that sociable guppy females that spend more time in groups have a tendency to copy the mate choice of their fellow females (White et al, 2017). Social females were shown to spend more time with a previously less preferred partner after seeing a familiar female spend time with that partner. While this is not a direct form of matching personality types between male and female, this does mean that in a social group of female guppies compared to solitary females, one preferred type of male could emerge, which could become a source of directed gene flow based on sociability, as a smaller variety of male genotypes would reproduce will all of these females.

Another study shows the influence of boldness in females of *Poecilia mexicana* on mate selection (Sommer-Trembo et al, 2016). This species has a strong diversity in subpopulations due to certain

subpopulations adapting their phenotype to sulphide springs in their habitat. The study shows the influence of personality traits like boldness/exploring on the willingness of non-sulfidic females to mate with sulfidic-adapted males. Results showed that bold, high exploratory females had a stronger preference for familiar, non-adapted males than shy, low exploratory females. This could possibly lead to a higher chance of hybridization between the sulfidic-adapted and the non-adapted phenotype, and subsequently lead to a subpopulation of hybrids, as previous studies have shown that hybridization can lead to rapid reproductive isolation based on sexual preference for other hybrids (Selz et al, 2013). While spontaneous hybridization between phenotypes is rare, this study shows that certain personality types are more prone to it than others.

There are also studies that show that matching personality types increases the fitness of a reproductive pair. In a study on eastern bluebirds, a species that provides biparental care for their offspring, results showed that pairs with similar nest defence strategies and aggression levels had increased reproductive success over other pairs (Burtka et al, 2015), and the coordination between the parents was more important than defence intensity on clutch quality. Another study on panda bears shows that matching certain personality types in panda bears increases reproductive success as well. In this case the personality types do not necessarily need to be similar to improve reproductive success. For example, low-excitation females and high-excitation females had better reproductive success than low-low or high-high pairs. It should be noted for this study that the pandas used for this study were all raised in captivity and are part of a breeding program, so these results might not necessarily translate over to a natural situation. Also, even though these studies show an increase in reproductive success based on personality matching, there is actually very little current evidence of assortative mating based on personality in the wild. One of the problems is that in quite some species, reproductive strategies are often correlated with a certain type of morph (St. Clair Yewers et al, 2016), for example bigger males being more aggressive, or the previously mentioned polymorphism/strategy relation in side-blotched lizards. This makes it hard to determine whether any assortative mating is based on the physique of the individual or the actual behaviour associated with it.

Concluding remarks

The possible influence of animal personality on ecological systems has been starting to get more and more attention in recent years, and with the sympatric model gaining acceptance as a viable model for speciation, new findings come out in an increasingly rapid rate. However, the direct correlation between different animal personalities and speciation is still an underdeveloped subject. In this thesis I have attempted to outline how treating animal personality as a possible factor in the speciation process can be a worthwhile basis for a study. In a theoretical sense, great progress has already been made towards creating ecological models that factor in animal personality, and showing correlations between consistently varying behavioural traits and their effect on migration, habitat choice and reproductive success. However, as is expected with such a recent line of study, concrete evidence is still few and far in between. In terms of habitat related studies, the line between correlation and causation is often hard to distinguish. Environment seems to influence personality as much as the other way around, which in first regards seems to be beneficial for speciation because of the positive reinforcement loop this effect might have, but at the same time begs the question to what extent there is a genetic basis to the habitat preference. If a personality based habitat preference is shaped mostly or purely by early life environment, it's hard to make a case for enhanced speciation speed as a consequence. In terms of sexual selection, it is easier to conduct studies in a controlled environment, and therefore concrete evidence was more widely available. There was clear evidence on personality influencing partner choice from the female perspective, but

usually not in regards to the personality of the male. While studies showed that matching certain personalities does increase reproductive success, little to no evidence was available for assortative mating based on personality. In species where you could make a case for this, mating behaviour is often tied to a certain morphology, which makes it difficult to make concrete statements about the basis of the preference.

That being said, I am confident that these current findings could pave the way for future study models on the possibility of personality affecting speciation. Speciation studies are a long term process that only recently gained big interest, and some of the published findings have been as recent as this month. For future study directions, I believe it is necessary to connect both the genetic basis of animal personality and its influence on migration/habitat choice within the same species, and to find a way to test for the influence of personality in the mating process while disconnected from the associated morph. I believe that in the future, animal personality will be commonly regarded as one of the driving factors of speciation.

References

Appels R., Nystrom-Persson J., Keeble-Gagnere G. (2014). Advances in genome studies in plants and animals, *Functional & Integrative genomics, 14(1),* 1-9

Benhaïm D., Skúlason S., Hansen B.R. (2003) Behavioural variation in juvenile Arctic charr in relation to body size, *Journal of Fish Biology, 62(6),* 1326-1338

Benkman C.W. (2016) Matching habitat choice in nomadic crossbills appears most pronounced when food is most limiting, *Evolution, 71(3),* 778-785

Bierbach D., Sommer-Trembo C., Hanisch J., Wolf M., Plath M. (2015). Personality affects mate choice: bolder males show stronger audience effects under high competition, *Behavioural Ecology, 26(5),* 1314-1325

Bolnick D.I., Amarasekare P., Araujo M.S., Bürger R., Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C., Vasseur D.A. (2011) Why intraspecific trait variation matters in community ecology, *Trends in Ecology & Evolution, 26(4),* 183-192

Calboli F.C.F., Byström P., Merilä J. (2016). A test for within-lake niche differentiation in the nine-spined sticklebacks (Pungitius pungitius) *Ecology and Evolution, 6(14),* 4753-4760

Canestrelli D., Bisconti R., Carere C., (2016). Bolder Takes All? The Behavioral Dimension of Biogeography, *31(1),* 498-499

Canestrelli D., Porretta D., Lowe W.H., Bisconit R., Carere C., Nascetti G. (2016). The Tangled Evolutionary Legacies of Range Expansion and Hybridization, *Trends in Ecology & Evolution, 31(9),* 677-688

Charmantier A., Doutrelant C., Dubuc-Messier G., Fargevieille A., Szulkin M. (2015) Mediterranean blue tits as a case study of local adaptation, *Evolutionary Applications, 9(1),*
135-152

Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations, *Ecology Letters, 12(3),* 197-209

Cloyed C.S., Eason P.K. (2017) Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans, *Royal Society Open Science, 4(3),* retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5383860/

Corl A., Davis A.R., Kuchta S.R., Comendant T., Sinvervo B. (2010) Alternative Mating Strategies and the Evolution of Sexual Size Dimorphism in the Side-Blotched Lizard, Uta Stansburiana: A Population-Level Comparative Analysis, *Evolution, 64(1),* 79-96

Corl A., Lancaster L.T., Sinervo B. (2012). Rapid Formation of Reproductive Isolation between Two Populations of Side-Blotched Lizards, Uta stansburiana. *Copeia, 2012(4),* 593-602

Cote J., Clobert J., Brodin T., Fogarty S., Sih A. (2010) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations, *Philosophical Transactions: Biological Sciences, 365(1560),* 4065-4076

Dall S.R.X., Bell A.M., Bolnick D.I., Ratnieks F.L.W. (2012) An evolutionary ecology of individual differences, *Ecology Letters, 15(10),* 1189-1198

Dix M.W., (1968) Snake Food Preference: Innate Intraspecific Geographic Variation, *Science, 159(3822)* 1478-1479

Dreiss AN, Antoniazza S, Burri R, Fumagalli L, Sonnay C, Frey C, Goudet J, Roulin A (2012) Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration, *Journal of Evolutionary Biology, 25(1),* 103-114

Dubuc-Messier G., Réale D., Perret P., Charmantier A. (2017). Environmental heterogeneity and population differences in blue tits personality traits, *Behavioural Ecology, 28(2),* 448-459

Duckworth R.A. (2009) The role of behavior in evolution: a search for mechanism, *Evolutionary Ecology, 23(4),* 513-531

Edelaar P., Siepielski A.M., Clobert J. (2008) Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology, *Evolution, 62(10),* 2462-2472

Gavrilets, S. (2014). Models of speciation, where are we now? *Journal of Heredity*, *105(S1)*, 743–755

Holtmann B., Santos E.S.A., Lara C.E., Nakagawa S. (2017) Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance, *Proceedings of the Royal Society: Biological Sciences, 284(1864) retrieved from* http://rspb.royalsocietypublishing.org.proxy-ub.rug.nl/content/284/1864/20170943

Karpestam E., Wennersten L., Forsman A. (2012) Matching habitat choice by experimentally mismatched phenotypes, *Evolutionary Ecology, 26(4),* 893-907

Keats B.J.B., Sherman S.L. (2013) Chapter 13 – Population Genetics, *Emery and Rimoin's Principles and Practice of Medical Genetics (Sixth Edition)*

Liedtke J., Redekop D., Schneider J.M., Schuett W. (2015). Early Environmental Conditions Shape Personality Types in a Jumping Spider, *Frontiers in Ecology and Evolution, retrieved from* https://www.frontiersin.org/articles/10.3389/fevo.2015.00134/full

Lil A. (1968). Spatial Organisation in Small Flocks of Domestic Fowl, *Behaviour, 32(4),* 258-290

MacKay J.R.D. & Haskell M.J. (2015). Consistent Individual Behaviour Variation: The Difference between Temperament, Personality and Behavioral Syndromes. *Animals, 5(3),* 455-478

Martin-Wintle M.S., Shepherdson D., Zhang G., Huang Y., Luo B., Swaisgood R.R. (2017) Do opposites attract? Effects of personality matching in breeding pairs of captive giant pandas on reproductive success, *Biological Conservation, 207,* 27-37

Morana N.P., Mossopa K.D., Thompson R.M., Wong B.B.M.(2016). Boldness in extreme environments: temperament divergence in a desert-dwelling fish, *Animal Behaviour, 122,* 125-133

Noor M.A.F., Feder J.L. (2006) Speciation genetics: evolving approaches, *Nature reviews Genetics, 7,* 851-861

Nosil P., Flaxman S.M. (2011). Conditions for mutation-order speciation, *Proceedings: Biological Sciences, 278(1704)* 339-407

Paris J.R., King R.A., Stevens J.R. (2015). Human mining activity across the ages determines the genetic structure of modern brown trout (Salmo trutta L.) populations, *Evolutionary Applications, 8(6),* 573-383

Réale D., Garant D., Humphries M.M., Bergeron P., Careau V., Montiglio P.O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population
Level, *Philosophical Transactions: Biological Sciences, 365(1560),* 4051-4063

Řežucha R., Reichard M., (2016). The Association Between Personality Traits, Morphological Traits and Alternative Mating Behaviour in Male Endler's Guppies, Poecilia wingei, *Ethology, 122(6),* 456-467

Rice W.R., Hostert E.E., (1993). Laboratory Experiments on Speciation: What Have We Learned in 40 Years? *Evolution, 47(6),* 1637-1653

Ricklefs R.E., Bermingham E., (2004). Application of Johnson et al.'s speciation threshold model to apparent colonization times of island biotas, *Evolution, 58(8),* 1664-1673

Robb G.N., Harrison A., Woodborne S., Bennett N.C., (2016) Diet composition of two common mole-rat populations in arid and mesic environments in South Africa as determined by stable isotope analysis, *Journal of Zoology, 300(4),* 257-264

Schuett W., Dall S.X.R., Kloesener M.H., Beaumer J., Beinlich F., Eggers T. (2014). Life-history trade-offs mediate 'personality' variation in two colour morphs of the pea aphid, Acyrthosiphon pisum, *Journal of Animal Ecology, 84(1),* 90-101

Schuett W., Tregenza T., Dall S.X.R. (2009). Sexual selection and animal personality, *Biological Reviews, 85(2),* 217-246

White D.J., Watts E., Pitchforth K., Agyapong S., Miller N. (2017) 'Sociability' affects the intensity of mate-choice copying in female guppies, Poecilia reticulate, *Behavioural Processes, 141(2),* 251-257

Selz O. M., Thommen R., Maan M. E., Seehausen O. (2013) Behavioural isolation may facilitate homoploid hybrid speciation in cichlid fish, *Journal of Evolutionary Biology, 27(2),* 275-289

Sommer-Trembo C.*,* Bierbach D., Arias-Rodriguez L., Verel Y., Jourdan J., ZimmerC., Riesch R., Streit B. and Plath M.(2016). Does personality affect premating isolation between locally-adapted populations? *BMC Evolutionary Biology, Retrieved from* https://bmcevolbiol-biomedcentral-com.proxy-ub.rug.nl/articles/10.1186/s12862-016-0712-2

Stamps J.A. (2015). Individual differences in behavioural plasticities, *Biological Reviews, 91(2),* 534-567

St Clair Yewers M., Pryke S., Stuart-Fox D. (2016) Behavioural differences across contexts may indicate morph-specific strategies in the lizard Ctenophorus decresii, *Animal Behaviour, 111,* 329-339

Sinervo B., Lively C.M. (1996) The rock-paper-scissors game and the evolution of alternative male strategies, *Nature, 380,* 240-243

Toscano B.J., Gownaris N.J., Heerhartz S.M., Monaco C.J. (2016) Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level, *Oecologia, 182(1),* 55-69

Via S. (2009). Natural selection in action during speciation. *Proceedings of the National Academy of Sciences of the United States of America, 106(1),* 9939-9946

Wolf M., Weissing F.J., (2012). Animal personalities: consequences for ecology and evolution, *Trends in Ecology & Evolution, 27(8),* 452-461

Xue Y, Wang Q, Long Q, Ng BL, Swerdlow H, Burton J, Skuce C, Taylor R, Abdellah Z, Zhao Y; Asan, MacArthur DG, Quail MA, Carter NP, Yang H, Tyler-Smith C (2009). Human Y chromosome base-substitution mutation rate measured by direct sequencing in a deep-rooting pedigree, *Current Biology, 19(17),* 1453-1457