

# **Anthropogenic influences on mating behaviour**

**An overview of the implications of human activities on mate choice in animals**

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## **Abstract**

Human behaviour has influenced the environment for the last centuries. The effect this has on mating behaviour has been studied only in several cases, even though mating behaviour stands at the basis of population dynamics in sexually reproductive species. In this review, I re-examine some of the studies which have been done to date on the impact of anthropogenic influences on mating behaviour. This impact may affect mate searching behaviour, so that individuals have a harder time finding a mate. It may also influence the assessment of a mate, for example by affecting the perception of signals individuals use to show their fitness. Finally, this impact may affect the decision on which is the best mate. This can be because the alteration of the environment may cause different mates to become indistinguishable from one another or because of a change in mate preference. I discuss the long term effects that these changes may have on species, focusing on the possible effects of increased hybridisation rate on species persistence and divergence. There are several studies which state that there is a negative impact on biodiversity due to hybrids, but there are also studies which suggest a possible positive influence of hybrids on speciation. I argue for a better understanding of the mechanisms by which hybridisation may influence populations so that we may make better predictions of species persistence and divergence. And so that we may mitigate the negative effects and possibly enlarge the positive effects.

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## Introduction

Human behaviour has been strongly influencing ecological systems, especially in the last centuries. This has been especially pronounced in the increase of several kinds of pollution (Diaz and Rosenberg, 2008; Longcore and Rich, 2004), habitat destruction (Tilman et al., 1994) and fragmentation (Fischer and Lindenmayer, 2007) and in the effects of global warming (McCarty, 2001). Humans also convert large patches of nature for agricultural use, resulting in more homogenous systems. These anthropogenic influences have created changes in species distribution and abundance. Although there are positive effects to be found from these anthropogenic influences, such as an increase in abundance of some bird populations (Siriwardena et al., 1998), anthropogenic influences are viewed to mainly have negative effects on biodiversity (Thomas et al., 2004; Vitousek et al., 1997). In order to mitigate the effects of human activities on nature, we need to understand the underlying processes.

In this review, I will look at anthropogenic influences on animal behaviour. There are many types of behaviour which are affected by humans. One of those types is mating behaviour. Since mating behaviour directly influences population dynamics, changes in this kind of behaviour can have tremendous impact on species (Dowling and Secor, 1997; Seehausen, 2006). This could possibly lead species to become threatened or go extinct. In the future it will be important to have a better understanding of the ways in which mating behaviour is affected by anthropogenic influences, since the impact of these effects is predicted to become larger (Parmesan and Yohe, 2003). By having a better understanding of the implications this has on mating behaviour, we might lessen this predicted impact on the affected species. Therefore, in this review, I will focus on the effects of anthropogenic influences on mating behaviour and changes in mate choice.

Firstly, there are several ways in which anthropogenic influences may affect a mating event. I will explore these ways so that we have an overview on the possible changes in mating behaviour humans may cause. I will also look into the effects on hybridisation. I will explain that when there is a decrease in preference for conspecifics, hybridisation between species might occur more frequently. Hybridisation may also occur more often when there still is a preference for conspecifics. If, due to a change in the environment, an individual becomes unable to express this preference, hybridisation may also occur more often.

Secondly, I will evaluate some examples and evidence that those changes have occurred in nature and that anthropogenic influences do cause hybridisation between closely related species. By this I will show that these effects influence the current ecology and that this influence will be a driving force for behavioural change and an increased number of hybridisation events in the future.

Lastly I want to raise the question of what effects the observed changes may have on species in the long term. Where the previous chapter has shown that the number of hybridisation events most likely will increase, this chapter focusses on the effects that this has in the long term on species. I will look into whether the changes might be mainly caused by plasticity and learning, or whether there might also be genetic change involved.

The latter could mean that the changes observed are persistent and might even lead to speciation or extinction in the future. This is interesting especially in the case of hybridisation, where introgression may cause great effects on the parent population's genetics (Crispo Erika E et al.; Rhymer and Simberloff, 1996; Seehausen, 2006).

## Ways in which mating events might be affected

For sexually reproducing species, mating events are events where males and females interact to decide whether they want to mate and produce offspring together. These events come with a specific behaviour. This behaviour often includes showing specialised courtship rituals. There is often a choosy sex and a chosen sex during mating events. Often, the chosen sex has to display its fitness and the choosy sex then decides which individual to mate with. There are also cases where the chosen sex forces the choosy sex to mate, but in most cases the choosy sex decides on the individual to mate with.

Mating behaviour has always been influenced by natural disturbances, such as changes in selection pressure, diseases and natural disasters. However, since humans have come to influence natural ecosystems such a large variety of ways (Vitousek et al., 1997), it is likely to think that humans will influence mating behaviour more strongly.

This mating behaviour depends on sensory signals. The chosen sex uses extreme signals such as coloration, size display, and song, and often a multitude of these signals (Candolin, 2003). These signals often display the chosen sex' fitness. It is proposed that the specific traits that are picked by the choosy sex, display the chosen sex' fitness (Emlen and Oring, 1977; Neff and Pitcher, 2005). Both sexes depends on their sensory input to decide which individual to mate with. This input can be altered by habitat change due to anthropogenic influences. When this happens, both sexes have to adapt to the new situation and often show different mating behaviour.

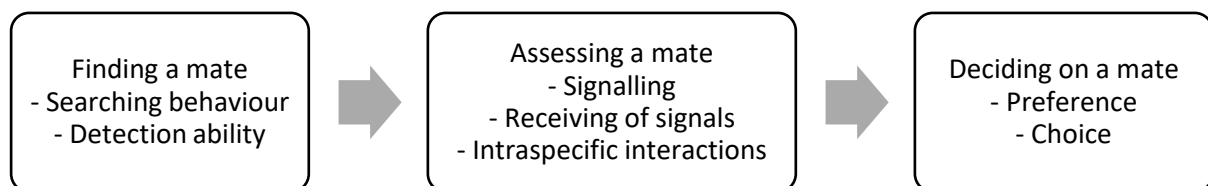


Figure 1: Ways in which a mating event may be altered

As seen in *Figure 1*, there are three different points where a mating event can be altered.

Firstly whilst finding a mate, to reproduce, an individual must first find a congener of the opposite sex. When the sensory input is disturbed, individuals might have a harder time locating a potential mate and therefore male-female encounters might become more rare. Some evidence for this has been found in Lusitanian toadfish, *Halobatrachus didactylus*, (Vasconcelos et al., 2007). Due to an increase in underwater noise, male signalling to females became masked. This caused a decrease in male-female encounters.

The way in which an individual searches for a potential mate might be altered as well. When the environment changes, the original searching method may become less effective or may have different fitness consequences, such as an increased predation. To overcome these

problems, some species change the way in which they search for mates. This has been shown for great tits, *Parus major*, (Slabbekoorn and Peet, 2003). Great tit males have been found to use higher pitch song to attract females, if anthropogenic background noise threatens to mask their original song.

Secondly, once a potential mate is found, the pair starts to assess one another. The chosen sex tries to court the choosy sex, often by showing one or more intense sensory signals. This signal might become less pronounced due to changes in the habitat. This happens for example in guppies, *Poecilia reticulata*, where both the amount of male colouration spots and the spots' colouration intensity decrease because of an increase in hormones in the environment (Baatrup and Junge, 2001).

Another role is played by interspecific interactions. When individuals of the chosen sex become less territorial or competitive due to a change in the environment, this may alter the mating behaviour as well. This is shown in three-spined sticklebacks, *Gasterosteus aculeatus*, for example (Bell, 2001) where an increase in oestrogenic hormones in the environment results in a lowered expression of territorial behaviour and aggression.

Finally, the decision whom to mate with might be affected by anthropogenic changes. If the habitat changes, the mate preferences of the choosy sex might also change. This could be so because the received signal is not a good representation of the fitness of the mate anymore. That this can have drastic effects is evident in spadefoot toads, *Spea bombifrons* and *Spea multiplicata*. During droughts females develop a preference for males of another species. Since their offspring hatches faster, this gives them a better chance of survival (Pfennig, 2007). In three-spined sticklebacks, *G. aculeatus*, it is shown that female preference for male colouration is lessened (Candolin et al., 2007). Due to an increase in algal growth, female perception of male nuptial colouration is decreased. This causes a lower selection pressure for male colouration.

Even if the preference does not change, the actual mate choice might still be affected. When the choosy sex cannot rely on the senses to see the difference between male signals, this can cause the mate choice to become more random since the choosy sex cannot differentiate fitter mates from less fit mates.

Alteration of a mating event might lead to a less pronounced choosy sex choice for conspecific individuals. This could be because of a change in choosy preference, when interspecific individuals show this trait better. It could also be because of the inability to choose on the preference. When an individual cannot distinguish different mates from each other, it may result in inability to distinguish conspecific mates from intraspecific mates. Especially since there are many closely related species where mainly the mating behaviour has diverted, (Gray and McKinnon). Lastly, because of a change in the signals chosen individuals use, they may show more similarity to intraspecific mates. This could also lead to an increased choice for intraspecific mates. When there are also encounters with the opposite sex of closely related species, this might result in a breakdown of the prezygotic isolation. This would result in hybridisation between the two populations and potential

introgression (Crispo et al., 2011). The effects this may have on population dynamics later in this review.

The change in mate preference can be genetic or plastic. When it is plastic, the change in preference will revert to the original preference if the environment also reverts back to the original situation. This shows that the choosy sex adapted its preference to the environmental changes by learning or plasticity. An example of this are the spadefoot toads, *S. bombifrons* and *S. multiplicata*, where females revert their preference to conspecific males if there is enough water available (Pfennig, 2007). Changes can also be genetic, this could cause the species to develop different behaviour that is persistent over time. I will discuss the possible effects of this on population dynamics later in the review.



Disturbance	Type	Environmental change	Affected trait	Mechanism	Consequence	Evidence
Climate change	Increased time of droughts	Smaller water pools available	Female mate choice	Females switch from preference for conspecific males to heterospecific males	Increase in hybridisation	Spadefoot toads, <i>S. bombifrons</i> and <i>S. multiplicata</i> , (Pfennig, 2007)
Direct habitat alteration	Habitat fragmentation	Smaller, isolated populations	Lower dispersal rate of males	Females encounter more related males	Increase in inbreeding	Agile antechinus, <i>Antechinus agilis</i> , (Banks et al., 2005)
			Male mate locating behaviour	Male switch of locating behaviour	Males use patrolling as main mate-locating behaviour	<i>Salamis parhassus</i> , (Bonte and Van Dyck, 2009)
Pollution	Noise pollution	Increase in background noise	Male signalling is masked by background noise	Decreased female ability to detect male signal	Lowered reproduction	Lusitanian toadfish, <i>H. didactylus</i> , (Vasconcelos et al., 2007)
		Increase in background noise	Male signalling is masked by background noise	Males switch to a higher pitch to avoid being overwhelmed by background noise	Males sing at a higher pitch	Great tits, <i>P. major</i> , (Slabbekoorn and Peet, 2003)
		Increased water turbidity	Female ability to detect male colour signalling	Decreased ability to choose for male colouration	Possible increase in hybridisation	Cichlids, <i>P. nyererei</i> , some <i>Neochromis species</i> , (Maan et al., 2010; Seehausen et al., 1997)
	Eutrophication	Increased water turbidity Increase in algal growth	Decreased female preference for male colouration	Decreased selection on male colouration	Sexual selection for male colouration is decreased	Three-spined sticklebacks, <i>G. aculeatus</i> , (Candolin et al., 2007)
			Increase in algal growth Increased acidity of water	Male capacity to monopolize multiple females	More evenly distributed females per male	Possible lower population fitness
		Females perception of male signals	Females show a weaker reaction to male signals	Increase in hybridisation	Swordtails, <i>Xiphoporus helleri</i> , (Fisher et al., 2006)	
	Chemical pollution	Increased acidity of water	Females show stronger perceptive ability for male olfactory signals	Females switch in preferred male signal from visual signals to olfactory signals	Different selection pressure on males	Three-spined sticklebacks, <i>G. aculeatus</i> , (Heuschele and Candolin, 2007)
			Increase in amount of hormones in water	Males become less aggressive to other males, less territorial	Lowered male fitness	Possible change in population growth rate
		Male colouration becomes less pronounced, lower male fertility	Decreased ability of females to detect fit males	lower number of offspring	Guppies, <i>P. reticulata</i> , (Baatrup and Junge, 2001)	

Table 1 shows some of the possible ways in which anthropogenic disturbances may alter mating behaviour.

Table 1: Overview of ways in which anthropogenic disturbances might influence mating events.

### **Evidence for the alteration of mating behaviour**

As is shown above, several effects may result from anthropogenic influences.

Firstly we will discuss evidence for the change in signals.

Secondly we will show examples of how signals can be perceived differently due to alteration of the transmission or perception.

Thirdly we will provide evidence that intrasexual interactions such as male-male interactions are also influenced.

Finally we will discuss some studies which show that anthropogenic influences can cause changes in mate preference.

### **Changes in signals**

One example of a change in signal comes from research in great tits, *P. major*. A large portion of the great tits, *P. major*, live close to human inhabited areas. Human-made heavy machinery and traffic produce a lot of background noise, which can mask the sounds that animals produce for their communication. Great tits, *P. major*, males use song to court females. When their song is threatened to be masked by anthropogenic sounds, they switch to a higher pitch (Slabbekoorn and Peet, 2003). Anthropogenic noise is mainly of a lower pitch so this helps them prevent their song from being masked. Presumably these higher notes come from their available repertoire, showing their plasticity to adapt to high background noise levels. This does not cause their territories to overlap, suggesting that they adapt their song to their territory instead of the other way around (Slabbekoorn and den Boer-Visser, 2006; Slabbekoorn and Peet, 2003; Slabbekoorn and Ripmeester, 2008; 2002). Since males which use higher pitches are perceived better, their mating success is higher than that of males which do not use higher pitches. (Slabbekoorn and Smith, 2002) Not all changes in signal are adaptive to environmental change. Male guppies, *Poecilia reticulata*, depend on brightly coloured orange spots to show their fitness to females (Houde, 1997). Due to an increase in antiandrogen hormones in the environment, male guppies develop less intense orange colouration (Baatrup and Junge, 2001). It has also been shown that their testes can become underdeveloped, having a negative effect on their sperm count. The presence of antiandrogens also decreases the time males spent on courting behaviour. Moreover, due to the colouration covering less area and having a lower intensity, females react less to the male courting (Baatrup and Junge, 2001). This shows how severe human influences can be to species.

### **Changes in signal transmission or perception**

The perception of signals might also be altered. This is shown in swordtails, *Xiphoporus helleri*. Since swordtails often co-occur with closely related species, Fisher et al. (2006) proposed that reproductive isolation relies on the females' ability to distinguish between conspecific and heterospecific males. When the concentration of Hyaluronic acid in the environment is increased due to toxic runoff from factories, females react less to the chemicals males use to attract females. This is either due to the Hyaluronic acid binding to those chemicals, or binding to female receptors. This has not been shown in the research. This results in a reduced female motivation to mate. Moreover, due to the higher level of Hyaluronic acid, the female preference for conspecific males was observed to disappear.

This resulted in an increased number of hybrids in the tested populations in the Río Panuco Basin in the northeast of Mexico (Fisher et al., 2006).

An example of how a change in transmission can alter mate choice is found in a cichlid species, *P. nyererei*. In these species, females prefer males that are brightly coloured, adapted to the local light environment. Species of cichlids living more to the surface develop a preference for brightly blue coloured males and deeper living species prefer red coloured males. Due to eutrophication, more particles are dissolved in the environment, altering the local light spectrum. This causes the sexual selection on colouration to relax, which decreases the male colouration intensity. Female preference for male colouration is also lowered, so much that they readily hybridise with males from other species. It is proposed that this would eventually cause the two species to dissolve into one hybrid species (Maan et al., 2010; Seehausen et al., 1997).

Even if hybridisation does not occur due to a change in signal perception, the population can still suffer from the environmental change that caused it. In the Lusitanian toadfish, *H. didactylus*, males use sound to attract females for mating. An increase in background noise due to intensified shipping caused these sounds to become masked, making it more difficult for the males to attract females (Vasconcelos et al., 2007). This could have a possible degradation of sexual selection as a result.

### **Changes in intrasexual interactions**

Not only male-female interactions may be influenced. Intrasexual interactions are also altered by anthropogenic influences. One example is the three-spined stickleback, *Gasterosteus aculeatus*, in which an increase in oestrogenic hormones in the environment results in a lowered expression of territorial behaviour and aggression (Bell, 2001). Due to this, it is speculated that individual male fitness can decrease and females cannot depend on territory size as an indication of fitness anymore.

Another example of this comes from sand gobies, *Pomatoschistus minutus*. In this species, the males have a territory with a nest and attract females to lay their eggs inside the nest. Under normal conditions, females favour large males with bright blue spots on their fins (Järvenpää and Lindström, 2004). There is competition between the males for the females and the bigger males usually monopolize several females. However, under turbid conditions, the females become more evenly distributed among males. Moreover, the average male size does also decrease, suggesting a relaxation in sexual selection on this trait (Järvenpää and Lindström, 2004).

### **Changes in preference**

Even if a signal is perceived properly, it will not be selected if the choosy sex changes its preference. It has been shown in several cases that this can happen due to a change in the environment. For example in three-spined sticklebacks, *G. aculeatus*, in the Baltic Sea, where females have switched their preference from depending mainly on visual signals to depending mainly on olfactory signals due to an increase in acidity of their environment (Heuschele and Candolin, 2007). This study was done on sticklebacks, *G. aculeatus*, from the Baltic sea. Due to increased eutrophication, sexual selection on visual signals decreases. (Candolin et al., 2007). The sea becoming more acidic caused the male chemicals to be

perceived better, causing the females to switch in preference so that they can still distinguish between males.

A more extreme example is that of the spadefoot toads, *S. bombifrons* and *S. multiplicata* (Pfennig, 2007). Hybridisation is often considered as a maladaptive situation which should be avoided. Spadefoot toads show that this is not always the case. During droughts, females of *S. bombifrons* show a higher preference for heterospecific males than in humid circumstances. *S. multiplicata*, whose males' preference is increased, have a shorter offspring development time. This causes an extreme increase in hybrid fitness during dry periods, when the pools both species live in can dry up. Even though hybrid offspring displays a much lower fitness under ideal environmental conditions, during drought it is so advantageous to have offspring which quickly develops that females from *S. bombifrons* readily accept heterospecific males. This change in preference is completely dependent on the amount of water available. Climate change is expected to make the deserts expand, therefore we can predict more hybridisation between the two species.

### **Long term consequences of anthropogenic influences**

In the previous parts I have shown that anthropogenic influences do influence mating behaviour. What are the possible long term consequences that follow from this change in behaviour?

If species are able adapt to short-term environmental effects this would be via plasticity, since genetic change cannot explain changes in an individual's behaviour. Adaptations to long-term environmental change, however can be explained by both plasticity and genetic change. The first adaptations will be plastic and when those plastic changes are persistent, they become embedded in the genetics of the species (Price et al., 2003).

In some species, like the spadefoot toad, *S. bombifrons* and *S. multiplicata* (Pfennig, 2007), it has been shown that the behavioural change is at least partially plastic and will revert to the original behaviour when the environmental circumstances also revert to the original state. However, most of the environmental changes caused by anthropogenic influences will likely be persistent (Vitousek et al., 1997).

Adaptation to changes in the environment may not only be plastic, but eventually also become imbedded in the species genetics. When this happens the species characteristics may become permanently altered.

As is seen in the three-spined sticklebacks, *G. aculeatus*, (Bell, 2001), anthropogenic influences may affect population fitness. Due to reduced male fertility and mating behaviour, the population produces less offspring as a whole and the offspring is also less fertile than populations in which no anthropogenic influences on the environment are present. This is also evident for guppies, *P. reticulata*, (Baatrup and Junge, 2001) and Lusitanian toadfish, *H. didactylus*, (Vasconcelos et al., 2007). For species that exist of only one or several populations, the resulted decrease in fitness can mean a serious threat to its existence (Burger and Lynch, 1995).

Not all species are affected by the change in environment. Most species seem to cope with new environmental stressors. This is visible in cichlids, *P. nyererei* (Maan et al., 2010), where

female preference is altered by an increase in water turbidity. Spadefoot toads, *S. bombifrons* and *S. multiplicata*, also show this kind of adaptive capacity (Pfennig, 2007) and so do great tits, *P. major*, (Slabbekoorn and Peet, 2003). When the change in environment is permanent, this might result in a change in the genetic composition of these species. What species can adapt to environmental change by plasticity and genetic change and what species cannot adapt is not entirely clear. It is suggested that the ability to adapt depends on the rate with which the environment is disturbed. (Hendry et al., 2008) Up to a certain level, phenotypic plasticity can keep up with the disturbance. How big a disturbance species can overcome, differs per species.

I have also shown some examples where hybridisation rates are increased, such as in cichlids, *P. nyererei*, (Maan et al., 2010; Seehausen et al., 1997), spadefoot toads, *S. bombifrons* and *S. multiplicata*, (Pfennig, 2007) and swordtails, *Xiphoporus helleri*, (Fisher et al., 2006). This can happen to species which are only separated by pre-zygotic isolation barriers. It is proposed that due to the environment becoming more homogenous, hybridisation rates will only increase more (Seehausen, 2006). Hybridisation can affect both parent species. Through introgression genes can flow from one parent population to the other, thereby altering the genetic composition of the parent species (Crispo et al., 2011). This could lead to several situations. The one most discussed and which most researches expect to occur is a hybrid swarm, where the number of hybrids vastly outnumbers one or both parental populations and due to the small chance of actually finding a conspecific mate, the extinction of one or both of the parent species (Crispo et al.; Rhymer and Simberloff, 1996; Seehausen, 2006). Especially at risk are species in situations where one of both parent populations is much smaller than the other, causing the small population to be outnumbered by hybrids, making them possibly go extinct (Crispo et al., 2011). This is not the only possible effect hybridisation may have on the long term. As is shown in some reviews (Dowling and Secor, 1997; Reyer, 2008), hybridisation may also provide positive effects. For example to small populations which suffer from inbreeding depression. Due to the influx of new genetic material, the inbreeding depression may be lifted, leaving a viable population. Moreover, it is stated that hybridisation might have been happening more often than observed (Dowling and Secor, 1997). Hybridisation can also create a population with a greater adaptive potential, which may be more a more regular event than is represented in current research.

Due to the genetics of both parent population mixing, new combinations may arise which are better suited to the changed environment. This could in the long run even lead to reproductive isolation, when hybrids don't reproduce with the parent species. This could be due to them being suited to a niche that was before then uninhabited by either parent species. If from this follows that hybrids do not co-occur with their parent species anymore, or if their mating preferences are so different that introgression does not occur, hybrids might develop postzygotic isolation over time (Dowling and Secor, 1997; Kawata and Yoshimura, 2000). Another way in which hybrids may become reproductively isolated, is when the offspring they produce with their parent species is unviable. This could eventually also lead to speciation.

## Discussion

The environment has hugely changed due to anthropogenic influences (Parmesan and Yohe, 2003), which has forced many species to adapt to new circumstances. This has resulted in changes in mating behaviour among a wide array of species, from fishes (Baatrup and Junge, 2001; Fisher et al., 2006; Heuschele and Candolin, 2007; Maan et al., 2010) to birds (Slabbekoorn and Peet, 2003) and amphibians (Pfennig, 2007). Although not all species show the capacity of adaptation to the new environmental factors, some species, like great tits, *P. major*, (Slabbekoorn and Peet, 2003) and spadefoot toads, *S. bombifrons* and *S. multiplicata*, (Pfennig, 2007) have shown to possess remarkable plasticity. It is suggested that when the environmental change is persistent, these adaptations may change the genetic composition of species via an increase in genetic variation in the new environment. When selection on this variation takes place, the genetic composition of species may be altered (Hoffmann and Merilä, 1999; Holloway et al., 1990).

Among the changes in mating behaviour are changes in the choosy sex's preference. This has been shown to increase the probability of two closely related species hybridising. Due to this hybridisation, it is proposed that one or both of the parent species may go extinct (Crispo et al.; Rhymer and Simberloff, 1996; Seehausen, 2006). However, there are also studies that state that hybridisation happens more often than perceived and that it may actually aid in speciation and keeping high levels of genetic variation within populations (Dowling and Secor, 1997; Kawata and Yoshimura, 2000).

The observed changes in behaviour may have long-term consequences for populations. Most species seem to be capable to adapt to the found environmental changes by altering their behaviour. However, plasticity has limitations. If the environmental change is too drastic species may not be able to adapt (Hendry et al., 2008), leading to a decreased fitness. This is found in several species which were not capable of fully adapting (Baatrup and Junge, 2001; Bell, 2001; Vasconcelos et al., 2007).

All in all, anthropogenic influences will most likely keep altering environments. This has already been shown to have negative effects on biodiversity (Thomas et al., 2004; Vitousek et al., 1997). Therefore it is important to understand the behavioural changes that follow from this alteration. By understanding the limits of plasticity and genetic adaptation better, we can allocate our resources to the species and ecosystems which are most threatened. This would allow us to keep a higher level of biodiversity with the current amount of resources available.

It has also been shown that hybridisation will occur more often due to the observed changes. Hybridisation has long been perceived as something undesirable and the view has been that it should be avoided at all costs. I would argue against this. Anthropogenic environmental change will increase the occurrence of hybridisation events, and trying to prevent this will cost a lot of resources. It has been suggested that hybridisation can have a negative impact on biodiversity (Crispo et al.; Rhymer and Simberloff, 1996; Seehausen, 2006), but there are also cases where hybridisation promotes biodiversity and genetic

variation in populations (Dowling and Secor, 1997; Kawata and Yoshimura, 2000). The long lasting consequences of hybridisation are poorly understood, therefore I would suggest to do more research into the effects of hybridisation. By creating a better understanding of the mechanisms by which hybridisation can cause extinctions or promote speciation and genetic diversity, we may employ hybridisation in the future in combination with other conservational techniques.

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### **References**

- Baatrup, E., and Junge, M. (2001). Antiandrogenic pesticides disrupt sexual characteristics in the adult male guppy *Poecilia reticulata*. *Environ. Health Perspect.* *109*, 1063.
- Banks, S.C., Ward, S.J., Lindenmayer, D.B., Finlayson, G.R., Lawson, S.J., and Taylor, A.C. (2005). The effects of habitat fragmentation on the social kin structure and mating system of the agile antechinus, *Antechinus agilis*. *Mol. Ecol.* *14*, 1789–1801.
- Bell, A.M. (2001). Effects of an endocrine disrupter on courtship and aggressive behaviour of male three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* *62*, 775–780.
- Bonte, D., and Van Dyck, H. (2009). Mate-locating behaviour, habitat-use, and flight morphology relative to rainforest disturbance in an Afrotropical butterfly. *Biol. J. Linn. Soc.* *96*, 830–839.
- Burger, R., and Lynch, M. (1995). Evolution and Extinction in a Changing Environment - a Quantitative-Genetic Analysis. *Evolution* *49*, 151–163.
- Candolin, U. (2003). The use of multiple cues in mate choice. *Biol. Rev.* *78*, 575–595.
- Candolin, U., Salesto, T., and Evers, M. (2007). Changed environmental conditions weaken sexual selection in sticklebacks. *J. Evol. Biol.* *20*, 233–239.
- Crispo, E., Moore, J.-S., Lee-Yaw, J.A., Gray, S.M., and Haller, B.C. (2011). Broken barriers: human-induced changes to gene flow and introgression in animals: an examination of the ways in which humans increase genetic exchange among populations and species and the consequences for biodiversity. *BioEssays News Rev. Mol. Cell. Dev. Biol.* *33*, 508–518.
- Crispo, E.E., Moore, J.-S., Lee-Yaw, J.A., Gray, S.M., and Haller, B.C. (2011) Broken barriers: human-induced changes to gene flow and introgression in animals: an examination of the ways in which humans increase genetic exchange among populations and species and the consequences for biodiversity. *BioEssays* *33*, 508–518.

- Diaz, R.J., and Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science* 321, 926–929.
- Dowling, and Secor, C. (1997). The role of hybridization and introgression in the diversification of animals. *Annu. Rev. Ecol. Syst.* 28, 593–619.
- Emlen, S., and Oring, L. (1977). Ecology, Sexual Selection, and Evolution of Mating Systems. *Science* 197, 215–223.
- Fischer, J., and Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280.
- Fisher, H.S., Wong, B.B.M., and Rosenthal, G.G. (2006). Alteration of the chemical environment disrupts communication in a freshwater fish. *Proc. R. Soc. B-Biol. Sci.* 273, 1187–1193.
- Gray, and McKinnon, J.S. (1998). Linking color polymorphism maintenance and speciation. *Trends Ecol. Evol.* 22, 71–79.
- Hendry, A.P., Farrugia, T.J., and Kinnison, M.T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* 17, 20–29.
- Heuschele, J., and Candolin, U. (2007). An increase in pH boosts olfactory communication in sticklebacks. *Biol. Lett.* 3, 411–413.
- Hoffmann, A.A., and Merilä, J. (1999). Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* 14, 96–101.
- Holloway, G.J., Povey, S.R., and Sibly, R.M. (1990). The effect of new environment on adapted genetic architecture. *Heredity* 64, 323–330.
- Houde, A.E. (1997). Sex, Color, and Mate Choice in Guppies.
- Järvenpää, M., and Lindström, K. (2004). Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 2361–2365.
- Kawata, M., and Yoshimura, J. (2000). Speciation by sexual selection in hybridizing populations without viability selection. *Evol. Ecol. Res.* 2, 897–909.
- Longcore, T., and Rich, C. (2004). Ecological light pollution. *Front. Ecol. Environ.* 2, 191–198.
- Maan, M.E., Seehausen, O., and Van Alphen, J.J.M. (2010). Female mating preferences and male coloration covary with water transparency in a Lake Victoria cichlid fish. *Biol. J. Linn. Soc.* 99, 398–406.
- McCarty, J.P. (2001). Ecological consequences of recent climate change. *Conserv. Biol.* 15, 320–331.



- Neff, B.D., and Pitcher, T.E. (2005). Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Mol. Ecol.* *14*, 19–38.
- Parmesan, C., and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* *421*, 37–42.
- Pfennig, K.S. (2007). Facultative mate choice drives adaptive hybridization. *Science* *318*, 965–967.
- Price, T.D., Qvarnstrom, A., and Irwin, D.E. (2003). The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. B-Biol. Sci.* *270*, 1433–1440.
- Reyer, H.-U. (2008). Mating with the wrong species can be right. *Trends Ecol. Evol.* *23*, 289–292.
- Rhymer, and Simberloff, D. (1996). Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* *27*, 83–109.
- Seehausen (2006). Conservation: losing biodiversity by reverse speciation. *Curr. Biol.* *16*, 334–337.
- Seehausen, O., vanAlphen, J.J.M., and Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* *277*, 1808–1811.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H., and Wilson, J.D. (1998). Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *J. Appl. Ecol.* *35*, 24–43.
- Slabbekoorn, H., and den Boer-Visser, A. (2006). Cities change the songs of birds. *Curr. Biol.* *16*, 2326–2331.
- Slabbekoorn, H., and Peet, M. (2003). Ecology: Birds sing at a higher pitch in urban noise - Great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* *424*, 267–267.
- Slabbekoorn, H., and Ripmeester, E. a. P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* *17*, 72–83.
- Slabbekoorn, H., and Smith, T.B. (2002). Bird song, ecology and speciation. *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.* *357*, 493–503.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., et al. (2004). Extinction risk from climate change. *Nature* *427*, 145–148.
- Tilman, D., May, R., Lehman, C., and Nowak, M. (1994). Habitat Destruction and the Extinction Debt. *Nature* *371*, 65–66.

Vasconcelos, R.O., Amorim, M.C.P., and Ladich, F. (2007). Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. *J. Exp. Biol.* *210*, 2104–2112.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., and Melillo, J.M. (1997). Human Domination of Earth's Ecosystems. *Science* *277*, 494.