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Parasite burden and reproductive success

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INNEHÅLLSFÖRTECKNING

SAMMANFATTNING

Fortplantningsförmågan är av yttersta vikt för att föra sina gener vidare och säkra artens överlevnad. En viktig del i detta är valet av partner, vid parning med ofördelaktig partner riskerar man få mindre framgångsrik avkomma än om man hade parat sig med en bättre partner. För att kunna göra dessa val används olika sexuella signaler, ornament, som viktiga hjälpmedel. Många studier har konstaterat en positiv relation mellan sexuella signaler och reproduktionsframgång, vilket innebär att med bättre, klarare och mer symmetriska ornament följer en högre reproduktionsframgång. Valet av partner görs oftast av honor och därför är det hanarna som bär ornamenten. Vidare har studier gjorts på huruvida parasiter kan påverka de sexuella signalerna men inte så många studier har gjorts som täcker hela kedjan, från parasiter till reproduktionsframgång. I detta arbete är min huvudsakliga frågeställning om det finns något generellt samband mellan parasitbelastning och reproduktionsframgång.

För det första är det viktigt att veta lite om parasitism och hur parasiter kan infektera värddjuren. Parasiter kategoriseras som ekto- och endoparasiter, d.v.s. parasiter som lever på respektive inne i kroppen på värddjuret. Ett fylum av endoparasiter är i högre grad representerat i artiklarna – apikomplexa. De apikomplexa parasiterna som förekommer i detta arbete är *Leucocytozoon* spp. och *Plasmodium* spp. Därutöver har en ektoparasit nämnts, *Carnus hemapterus*, fylum atropoda.

För det andra vill man undersöka effekten av infektion på värddjuret. En hög parasitbelastning förbrukar energi och resurser av värddjuret som därmed inte har råd att producera lika iögonfallande sexuella signaler och färgstarka ornament, detta leder till en lägre chans för parning. Det har visats att ornament spelar en viktig roll i sexuell selektion och valet av partner, som ärliga signaler på kvalitet.

Sammanfattningsvis, majoriteten av artiklarna pekar i samma riktning och jag kan utifrån det dra slutsatsen att parasiter med stor sannolikhet påverkar sexuella signaler på ett negativt sätt. Detta leder då till en minskad chans för parning och därmed lägre reproduktionsframgång. Dock finns det meningsskiljaktigheter i frågan och vissa författare hävdar att det finns ett positivt samband mellan parasitbelastning och sexuella signaler vilket då skulle gynna reproduktionsframgången.

Nyckelord: parasiter, parasitbelastning, reproduktion, reproduktionsframgång, sexuella signaler, ornament

SUMMARY

Reproduction is fundamental for passing on genes and secure species survival. One crucial point of this is mate choice, mating with an unbeneficial partner, they risk less advantageous offspring than if a better mate had been chosen. To be able to make these choices, sexual signals, or ornaments, are very useful tools. Many studies have concluded the positive relationship between sexual signals and reproductive success, meaning that with better, brighter and more symmetric ornaments comes a higher reproductive success. Females are usually the ones that decide who is allowed to mate with them, therefore it is the males that carry ornaments. Additionally, studies have been made on how parasites can affect these ornaments but not many studies have covered the whole path, from parasite to reproductive success. For this work my main question is if there is any general correlation between parasite burden and reproductive success.

Firstly, it is important to know some basic background about parasitism and how parasites can infect their host. Parasites are categorized in two ways, ecto- and endoparasites, i.e. parasites living on the surface respectively on the inside of the hosts' body. One phylum of endoparasites has been mentioned more trequently than others among different studies - apicomplexans. The apicomplexan parasites presented in this work are *Leucocytozoon* spp. and *Plasmodium* spp. Additionally, one specific ectoparasite occurs, *Carnus hemapterus*, phylum arthropoda.

Secondly, the effect of parasite infection on the host. Higher parasite burden takes energy and resources from the host who thereby cannot afford to invest as much in sexual signals or brightly colored ornaments. This will lead to lower chance for mating, it has been shown that ornaments play an important role in sexual selection and mate choice, they act as honest signals for quality.

To summarize, a majority of the studies presented in this work point in the same direction and I can from them conclude that parasites most likely affect sexual signals negatively, leading to lower chance for mating and thereby lower reproductive success. Though, there are differences in opinion and some authors state that there is a positive correlation between parasite burden and sexual signals, in which case reproductive success would benefit.

Keywords: parasites, parasite burden, reproduction, reproductive success, sexual signals, ornaments

INTRODUCTION

No matter what species, the drive to reproduce is fundamental for passing on genes and secure species survival. It is of great importance to choose a healthy mate, to do this, sexual signals or ornaments come in handy. They have been shown to act as honest signals for fitness (Badas *et al*., 2017, Schluter *et al*., 1998, Taggart and Schultz, 2017, Meszaros *et al*., 2018, Chakarov *et al*., 2008, Saks *et al*., 2003) and because they are visual, their role can be easily evaluated in experiments.

Parasitism is a type of symbiotic relationship where one organism benefits on the cost of a host, mostly without killing it. There are two types of parasites, endo- and ectoparasites, which live inside respectively on the surface of the body. Parasites are tightly connected with its host and depend on the hosts' health and nutritional status for its own survival. Parasites and hosts are co-evolving and either they have a conflict relationship or a mutualistic, depending on how resources are distributed between them.

Not many studies have been made on how parasites affect reproductive success; instead I have focused on how parasites affect these sexual signals and their direct relation to reproductive success. Ornaments will here be used as a true indicator of reproduction success, based on the work of several authors. (Badas *et al*., 2017, Schluter *et al*., 1998, Taggart and Schultz, 2017, Meszaros *et al*., 2018, Chakarov *et al*., 2008, Saks *et al*., 2003). There will also be some examples of studies where the authors have looked into the relationship between parasites and reproduction.

My main question is if there is any general correlation between parasite burden and reproductive success.

MATERIAL AND METHODS

Web of Science and all databases connected were used for this work. Search phrases:

1. "parasite* OR parasite load OR parasite burden AND reproduct* OR reproductive success NOT human* OR child*" on February 9th 2018, 125 776 hits
2. "parasite* OR parasite load OR parasite burden AND reproduct* OR reproductive success AND bird* OR avian*" on February 10th 2018, 14 553 hits
3. "parasite* OR parasite load OR parasite burden AND reproduct* OR reproductive success AND deer* OR *cervidae*" on February 10th 2018, 1 358 hits

For each of these search results, the first 100 articles were checked.

Furthermore, searches on parasitism in general were also made, in Web of Science as well:

4. "endoparasitism" on February 13th 2018, 507 hits
5. "ectoparasitism" on February 13th 2018, 802 hits

For search number 4 and 5 the first 50 articles each were checked. This did not result in any information about parasitism in general so books were also used.

Additionally, further sources have been picked from articles' references that were found relevant.

LITERATURE REVIEW

Parasitism

Parasitism is a type of symbiotic relationship (Bush *et al*., 2001) and according to Britannica (2016) parasitism is the relationship that occurs between two different species, plants or animals, and where one of them benefits on the cost of the other, often not by killing the host. Parasites takes energy and resources from its host who thereby does not get as much for itself as it is producing (Toft *et al*., 1993, Reece *et al*., 2011). The host does not usually die from being exposed to parasites even though it can occur (Reece *et al*., 2011).

Parasites can be categorized into endoparasites which live inside its host and ectoparasites which live on the surface of its host (Britannica, 2016, Reece *et al*., 2011, Bush *et al*., 2001). The endoparasites can in turn be categorized in intercellular which live inside body cavities but not inside cells and intracellular which live inside the hosts cells (Britannica, 2016).

The group endoparasites contain cestodes, nematodes, trematodes and protozoa as well as viruses and many bacteria whilst ectoparasites contain arthropods and monogenans (Bush *et al*., 2001, Taylor *et al*., 2007).

Throughout this work one will notice that the apicomplexan parasites are more frequently used to test correlations to ornaments, sexual signals and reproductive success than other phylum. Apicomplexa are endoparasites, intracellular protozoa, that have both sexual and asexual phases (Taylor *et al*., 2007). The apicomplexan parasites in this work are *Leucocytozoon* spp. and *Plasmodium* spp.

Leucocytozoon spp. and *Plasmodium* spp. are blood parasites, causing avian malaria in the tropics, in wild and domestic birds. They are transferred by dipteran flies but the exact vector differs between different species (Taylor *et al*., 2007). *Anopheles* spp. is vectors for *Plasmodium* spp. (Bush *et al*., 2001). Belonging to the family *Plasmodiidae* (see *Table 1* for full taxonomy). The insect vector introduce sporozoites to new hosts when feeding on them. Within the host, different species infect the host in different ways. In general, they occupy tissue cells as well as blood cells and when mature they move to the plasma to enable them to get eaten by a vector, for example by destroying the blood cell they occupies (Taylor *et al*., 2007). Insect vectors feed on the host blood and ingest parasites at the same time. Within the vector a zygote is formed which then elongates into an ookinete. These ookinetes travel through the gut wall and some form subspherical oocyst on the outer wall of the gut. Sporozoites are then formed and are spread in the body cavity; sporozoites will eventually end up in the salivary glands, from where they get injected into a new host when the vector takes a blood meal (Taylor *et al*., 2007).

Table 1. Taxonomy of endoparasites

	Leucocytozoon spp.	*Plasmodium* spp.
Phylum	*Apicomplexa*	*Apicomplexa*
Order	*Haemosporida*	*Haemosporida*
Family	*Plasmodiidae*	*Plasmodiidae*
Genus	*Leucocytozoon*	*Plasmodium*

Although the details vary between different species of apicomplexan parasites, they all follow a general life cycle shown in *Figure 1* (Bush *et al*., 2001). All apicomplexan parasites have sexual as well as asexual phases. Sporozoites grow to trophozoites which then forms merozoites. Merozoites will eventually differentiate into gametes, micro and macro. In time one micro will fuse with one macro to form a zygote after which meiosis can occurs (Bush *et al*., 2001).

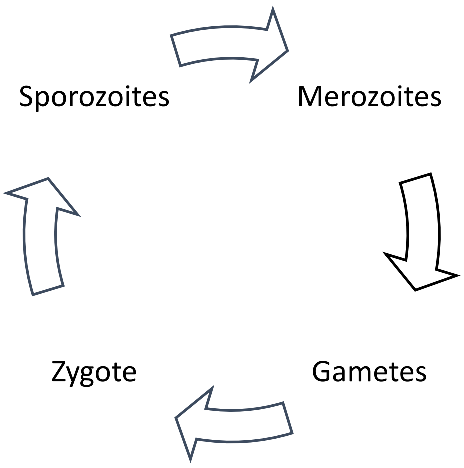

Figure 1. General life cycle of apicomplexa parasites, inspired by diagram by Bush et al. (2001)

One ectoparasite, *Carnus hemapterus*, belonging to the family *Carnidae* (see *Tabell 2* for full taxonomy) has been mentioned. This is a dipteran parasite (Bush *et al*., 2001). In many dipteran parasites only females are parasitic and which stage of development that is infective varies, it can be either larval or adult stage. Not only can they cause problem *per se* but they can also be vectors for other parasites which may be transferred during blood feed (Bush *et al*., 2001). Every female produces a relatively low number of larvae but the survival rate is high. They are present worldwide and can be active both day and night, depending on species, some being host specific whilst others are generalists (Bush *et al*., 2001).

Tabell 2. Taxonomy of ectoparasites

	Carnus hemapterus
Phylum	*Athropoda*
Order	*Diptera*
Family	*Carnidae*
Genus	*Carnus*

Genetics of the host plays an important role in if it gets infected or not, and if infected, how well it can handle it (Toft *et al*., 1993). Parasites are tightly connected with their hosts and dependent on them surviving long enough for the parasite to reproduce, if the host die so is the parasite likely to do (Bush *et al*., 2001, Toft *et al*., 1993). Parasites and hosts are coevolving, evolution in opposite direction result in conflict in resources. In contrast, evolution in the same direction, result in benefits for both (Toft *et al*., 1993). Toft *et al*. (1993) questioned if that, even though parasites and hosts can have a mutualistic relationship, isn't the parasite in the end still affecting the hosts' fitness negatively.

There are two ways in which co-evolution between host and parasite can occur. Firstly, the tolerance of the host prevents some of the negative effects of pathogens to happen and secondly, when a host is infected it can attack pathogen replication and thereby win time for self recovery, although this can also affect the hosts' fitness (Kutzer *et al*., 2018).

Sexual signals and reproductive success

There are different types of sexual signals; chemical, acoustic and visual. Ornaments, like coloration is a type of visual signal (Meszaros *et al*., 2018). Ornaments are described as different characteristics in the appearance of a specie; the symmetry of certain traits (Schluter *et al*., 1998, Brown and Brown, 2002, Taggart and Schultz, 2017), plumage coloration (Kruger *et al*., 2001, Saks *et al*., 2003, Chakarov *et al*., 2008, Badas *et al*., 2017, Chakarov *et al*., 2017, Badas *et al*., 2018), eggshell coloration (Martinez-de la Puente *et al*., 2007, Martinez-Padilla *et al*., 2010, De Coster *et al*., 2012, Badas *et al*., 2017) or other body colorations (Meszaros *et al*., 2018).

These ornaments act as sexual signals which are used, mostly by females but also by males, to choose mates for reproduction (Andersson, 1994, Schluter *et al*., 1998, Saks *et al*., 2003, Badas *et al*., 2018, Meszaros *et al*., 2018). In general it has been shown that ornaments play an important role in sexual selection because they often work as true signals for male quality, this is because ornaments are costly to produce (Andersson, 1994, Johnstone, 1994, Schluter *et al*., 1998, Saks *et al*., 2003, Chakarov *et al*., 2008, Badas *et al*., 2017, Taggart and Schultz, 2017, Meszaros *et al*., 2018). Studies also indicate that the more ornamented a male is, the more immunocompetent he is (Andersson, 1994, Saks *et al*., 2003). A less impressive display will reduce the males' chances of reproduction, due to reduction in chances to impress females and his order in the dominance hierarchy (Toft *et al*., 1993, Andersson, 1994).

Some examples

Blue tit (Cyanistes caeruleus)

Badas *et al*. (2017) studied the correlation between the males' quality and eggshell pigmentation in the blue tit, *Cyanistes caeruleus*. Eggshell pigmentation can be used as a post-mating sexual selection trait (De Coster *et al*., 2012) and Badas *et al*. (2017) looked at the males' display of his plumage, as a true sign for his quality. Their theory is that pigmented eggs laid by females are a result of a weak male not providing enough food for his female. They did show that females with poorer males did lay more pigmented eggs than those with wealthier conspecifics (Badas *et al*., 2017) and this was also concluded by Martinez-de la Puente *et al*. (2007). Pigmentation on eggshells is thus correlated with health status of the males and Badas *et al*. (2017, pp.7-8) stated *"more pigmented eggs generally having paler and more parasitized fathers".*

Sanz and Garcia-Navas (2009) writes that female quality can also be shown in eggshell coloration, this is because the pigment biliverdin is an antioxidant so more colored eggs tend to indicate higher antioxidant-producing capacity by the female. Further Sanz and Garcia-Navas (2009) explains that egg spottiness increases when female condition deteriorates, these females are often more extent infected by the blood parasite *Leucocytozoon* (Badas *et al*., 2017).

Common buzzard (Buteo buteo)

The publication *"Immune response link parasite genetic diversity, prevalence and plumage morphs in common buzzard"* by Chakarov *et al*. (2017) described how differences in plum pigmentation in the common buzzard, *Buteo buteo*, correlated with the immunological statuses of the birds. The pigmentation varies naturally within the common buzzard, from light to dark and with intermediate variants. Chakarov *et al*. (2017) states that intermediate pigmented birds can have up to two times greater reproductive success during their lifetime than the other types of pigmentations.

Sailfin molly (Poecilia latipinna)

"Female preference for symmetrical vertical bars in male sailfin mollies" written by Schluter *et al*. (1998) describes how female sailfin mollies, *Poecilia latipinna*, choose their mates depending on symmetry in male sailfin mollies vertical bars. Females uses males ornaments to determine whether he is of good quality or not, and therefore if he will be a good mate or not. In sailfin molly it is the vertical bars in males that accounts for the ornaments and thereby the visual signals for females. These bars have been shown to act as a true signal for male quality (Schluter *et al*., 1998). It has been shown that symmetrical bars are highly important for female selection, in contrast to total number of bars which does not seem as important, and when tested, females prefer males with vertical bars rather than males without. Schluter *et al*. (1998) also found a negative correlation between the amount of bars and variation in asymmetry, more bars meant more symmetry and the more symmetrical bars males had, the more females liked it. Schluter *et al*. (1998) concludes that symmetric bars are an indication

of good quality in sailfin mollies. Even if bars acts as true signals, males can try to cheat during courtship, this by swimming around the female in only one direction, letting her see only one side of him (Schluter *et al*., 1998).

This is supported by the work of Johnstone (1994) as well as Swaddle and Cuthill (1994), in which they state that females prefer males that are more symmetrical and that the degree of fluctuating asymmetry is directly connected with male quality. Furthermore, it is explained that in some species the level of asymmetry can be heritable and also correlated with other fitness measures. Swaddle and Cuthill (1994) argues that fluctuating asymmetry increases when individuals have a hard time to handle environmental distress and also that those higher quality individuals can afford to both produce bigger and brighter ornaments as well as preventing asymmetry.

Parasites effect on sexual signals

The influence that parasites have on its hosts varies, as stated earlier, and one attribute shown to be affected is sexual signals, or ornaments, which in turn plays an important role in sexual selection and mating and thereby reproductive success. More parasites will also result in weaker immunological status, energy is needed for fighting off the infection and less energy can therefore be used to establish ornaments (Andersson, 1994, Brown and Brown, 2002, Martinez-de la Puente *et al*., 2007, Martinez-Padilla *et al*., 2010, De Coster *et al*., 2012, Chakarov *et al*., 2017, Badas *et al*., 2018). Andersson (1994) concludes that males with the lowest parasite burden will get picked more often by females than more parasitized males.

The Hamilton and Zuk hypothesis from 1982 suggests that males with heritable parasite resistance also have some secondary sexual traits, like bright coloration, which is visual for others and used to determine mate choice (Andersson, 1994). These secondary sexual traits have, according to this hypothesis, coevolved with parasitic infections and their only role is to express the males immunological status (Hill and McGraw, 2006).

Some examples

Common buzzard (Buteo buteo)

As described earlier, Chakarov *et al*. (2017) looked into parasite infection and immunological status in different plumage morphs in common buzzard, *Buteo buteo*, light, intermediate and dark. They found a strong correlation between these two variables with intermediate colored birds having the best immunological status of the three. Dark nestlings are often more infected with the ectoparasite *Carnus hemapterus* and light nestlings with the blood parasite *Leucocytozoon* than the other morphs (Chakarov *et al*., 2017). In this study, Chakarov *et al*. (2017) concluded that the intermediate colored birds did show a stronger anti-inflammatory reaction than the other two morphs and argued that this might be one reason for their higher reproductive success.

Blue tit (Cyanistes caeruleus)

Badas *et al*. (2018) looked into coloration in the feathers of the blue tit, *C. caeruleus*, and how that associates with parasite load and body condition. A male less infected by *Plasmodium* spp. showed brighter white colored cheek feathers than those with higher parasite burden.

Males with whiter cheeks is stated to be in better condition and get higher reproductive success and they prefer to pair with females that also had more white cheeks than others. Badas *et al*. (2018) showed that the look on the white cheek varied a lot between pre- and post-moulting, depending on how infected the birds were by *Plasmodium* spp., and that the color of the white cheek does correlate with body condition and amount of plasmodium parasites while breeding.

Eggshell pigmentation

It is believed that pigmentations on eggshells can reflect female quality and therefore act as a post-mating sexual selection trait (De Coster *et al*., 2012). More pigmentation can indicate stronger female but it can also be an outcome of anemia and thereby weaker conditioned females. In a study by De Coster *et al*. (2012) it is stated that high parasite burden will result in darker spots on eggshells, and females with higher parasite load will get more severe anemia. Similarly, Martinez-de la Puente *et al*. (2007) did get a negative correlation between number of spots on eggshells and the females' health status. In contrast to these findings, Martinez-Padilla *et al*. (2010) state that females lay more pigmented eggs if they mate with males who are more resistant to infections and it is the male condition that determines the eggs pigmentation. It is probably costly to produce more pigmented eggs but even so, the authors says that this cannot be explained by female condition, but only by male condition (Martinez-Padilla *et al*., 2010). Males in better condition can afford greater and more colorful ornaments which is an important aspect in sexual selection. If males have the ability to put effort into great ornaments they will probably have enough energy to fight off infections as well. Females who mate with males of lower quality lay less pigmented eggs (Martinez-Padilla *et al*., 2010). The subject will be further discussed in the discussion section.

Asymmetry

Ectoparasites cause increased bilateral asymmetry of naturally selected traits in a colonial bird, cliff swallows, *Petrochelidon pyrrhonota*, as shown by Brown and Brown (2002). They show that level of asymmetry is positively correlated with parasite load. This asymmetry is likely due to nutritional stress caused by the parasitic infection and the asymmetry in turn will lead to lesser foraging ability because flight abilities is affected and therefore the parasites will cause a reduction in fitness for the birds (Brown and Brown, 2002). In their study, Brown and Brown (2002) showed that the level of asymmetry lowered when they removed ectoparasites in juvenile cliff swallows, but the underlying mechanisms for how parasite infection leads to decrease in symmetry are still unknown. In general, asymmetry is used to measure quality and condition of individuals and this phenomenon has also been seen in fish from polluted waters that got more asymmetric in gill rakers and fin rays than conspecifics from non-polluted waters. Brown and Brown (2002) note that there have been several studies on parasite load and asymmetry that have showed positive correlations.

Furthermore, Taggart and Schultz (2017) explains that ectoparasitism can lead to asymmetry in plumage, which they saw in trials with the New Holland honeyeaters, *Phylidonyris novaehollandiae*. Consequently, the lack of symmetry affects the birds' reproductive success negatively as it plays an important role in sexual selection (Taggart and Schultz, 2017). The birds are also at greater risk of dying, especially if it is feathers on wings or tail that is damaged, causing it to become an easier pray (Taggart and Schultz, 2017).

Studies on parasites effect on reproductive success

Studies have shown negative relationships between parasitism and reproductive success in different species (Toft *et al*., 1993, Andersson, 1994, Taggart and Schultz, 2017, Hoi *et al*., 2018). Reduction in reproductivity can be explained by lower condition of the host due to less available energy, which is used by the immune system to fight off the infection. Parasites can also compete with the host for its recourses that it normally would have used to, for example, grow better immunity (Hoi et al., 2018). Another theory is that infected animals cannot afford to have great displays, for example a magnificent plumage in birds, and this will lead to less reproductivity (Toft *et al*., 1993).

Some examples

Birds

The common buzzard, *B. buteo*, is a well-studied species on the subject and Chakarov *et al*. (2008) showed that in offspring from intermediate colored parents, prevalence of the blood parasite *Leucpcytozoon* was lower than in offspring from lighter or darker parents. Resistance to parasitic infections is heritable (Andersson, 1994). Intermediate colored buzzards have the best reproductive success whilst light and dark morphs both have a lower reproductive success. If a light and a dark bird should mate they would get intermediate colored chicks that would be more beneficial than if they would mate with similar colored birds (Kruger *et al*., 2001). Further, if males are heavily infected they will not have enough energy for raising chicks, during the first weeks it is their responsibility to provide the chicks with food and if they are not strong enough to hunt, their reproductive success will decrease and Chakarov *et al*., (2008) state that dark colored males mostly produce less healthy chicks. It is the amount of melanin that determines the coloration of the bird. Melanin is a pigment that also has been suggested to work as antimicrobial substance. More pigment should lead to stronger defense against infections (Chakarov *et al*., 2008). As has been mentioned before, this does not seem to be the case because the intermediate coloration has the greatest life reproductive success (LRS). Chakarov *et al*. (2008) showed significantly differences in LRS between the three colorations as well as between males and females, with the light and dark males having significantly lower reproductive success than the intermediate ones. Even though dark birds have more melanin they did show lower resistance to infections. One explanation might be that dark individuals absorb more heat from the sun and by that attract more parasites (Chakarov *et al*., 2008).

Another study, by Skas *et al*. (2003), looked at plumage coloration in male greenfinches, *Chloris chloris*, and how that affects female choice of a mate. It is beneficial for females to mate with strong males, to ensure this females chose their mate depending on the males ornaments, a male with greater ornaments are strong and can resist parasitic infections better, he will therefore pass on good genes to his offspring (Saks *et al*., 2003). A male that has less beneficial genes and a greater risk of being affected by parasites will not afford to have great ornaments and will thereby not get top-selected by females. One problem with sexual selection on plumage coloration is the fact that it reflects previous health of the male rather than his current health state, for example he might have caught a parasitic infection after the growth of the plumage. Saks *et al*. (2003) confirms that males with brighter coloration has lower parasite burden and that females rather mate with more colored males. In contrast, Saks *et al*. (2003) highlights that some studies have shown the opposite relationship, that birds with more ornamentation actually have a greater parasite burden.

A study of nestling European Bee-eaters, *Merops apiaster*, by Hoi *et al*. (2018) shows that infection with *C. hemapterus* in early life will result in lifelong reduction in fitness.

Other species

Apart from birds, this phenomenon has been shown on several other types of species, here are a few examples:

Studies on lizards by Meszaros *et al*. (2018), shows that males put energy on sexual signals to increase their chances to mate but this is at the cost of survival ability and thus, these signals can be true indicators of the males' quality. As an example the males of *Lacerta viridis* has a blue throat which correlates negatively with blood parasite infections and therefore works as a sexual selected signal (Meszaros *et al*., 2018).

Kutzer *et al*. (2018) showed a higher reproductive cost of higher *Pseudomonas entomophila* loads. Some *Drosophila melanogaster* was infected with *P. entomophila* and some with *Lactococcus lactis*, both opportunistic bacteria. Kutzer *et al*. (2018) saw that infection with *P. entomophila* resulted in less reproductive success.

DISCUSSION

Several studies concludes that ornaments or sexual signals play important roles in mate choice, like Schluter *et al*. (1998) showed in sailfin mollies, females are more likely to choose a male with ornaments, vertical bars, than one without. This indicates that the bars play an important role in sexual selection and truly are an honest signal for male quality. Females need these signals to determine whether a male is good enough to mate with or not.

Not always does this seem to work as we think, as in common buzzards, studied by Chakarov *et al*. (2008), intermediate colored buzzards are shown to have highest immunocompetence as well as the highest reproductive success but they also explains how the pigment melanin is suggested to work as a antimicrobial substance. This would mean that darker individuals should have the best defense against pathogens, due to the highest levels of melanin. Though, one cannot make any conclusions on parasitic infestation regarding how well an individual can withstand bacterial infections, so this does not really contribute to the summation of this review.

When it comes to eggshell pigmentation, there are quite some differences in opinion. De Coster *et al*. (2012) state that eggshell pigmentation is correlated with female condition, though they say that more pigmentation can be a result from both strong females as well as less healthy ones, e.g. females with anemia. The latter correlation was also determined by Martinez-de la Puente *et al*. (2007). In contrast to this, Martinez-Padilla *et al*. (2010) states that eggshell pigmentation does not depend on female condition but male only. This indicates that not enough studies have been made on the subject and one cannot be certain of whether eggshell pigmentation is due to female or male condition or due to wealth or distress, regardless of sex.

When combining the results from several studies on the subject, for example Toft *et al*. (1993), Andersson (1994) Saks *et al*. (2003), Taggart and Schultz (2017), Chakarov *et al*. (2008), Hoi *et al*. (2018), Kutzer *et al*. (2018) and Meszaros *et al*. (2018) a pattern of negative influence of parasites on reproduction success does seem to appear. Though, some authors argue that positive correlations between parasite burden and sexual signals have been seen, for example Saks *et al*. (2003) discuss that there have been studies which show a positive correlation between the two.

Though this review is limited in content, it covers some studies and highlights that a trend can be seen in correlations between parasite burden and reproductive success, it also shows that more information is required and further studies on the subject are necessary to obtain a better overall picture on this particular subject. One cannot be certain which parameter affects what and what the interaction looks like. Even though a negative correlation can be seen between parasite burden and reproductive success it does not mean that the two affect each other, nor if they are causal to each other. Maybe both are the result from some other factor, like genetic variation, which leads to lower health status which in turn leads to both higher parasite load as well as a lower reproductive success. In the example with common buzzard, Kruger *et al*. (2001) discuss the possibility of linked genes so the plumage coloration is only a visual trait that has nothing to do with the actual fitness.

To get an even bigger picture more studies on what kind of parasite is of greatest effect on reproductive success is needed. When reading articles for this work, only three different types of parasites showed up, two endoparasites belonging to the phylum apicomplexa and one ectoparasite belonging to the phylum athropoda, this can be considered a too small sample size for any conclusions to be made.

To know how parasites affect animal reproduction is of great importance in domestic animal medicine as well as in wildlife medicine. This work focuses on wildlife animals and is of little importance for clinical veterinarians. Rather, it can serve as a source of information for veterinarians and others working with wildlife management. In general, the more is known, the better methods can be developed and the more knowledge we have, the more understanding we will get for species dynamics and ecosystems. This can be used in further research and management. Even though this work focuses on wildlife animals and birds in particular, I think the principle addressed is applicable on a wide range of species, both wild and domestic.

In conclusion, parasites tend to negatively correlate with reproductive success, there does however seem to be some doubt about the direct causation. What is certain though is that ornaments act as honest signals for individual quality and are in relationship with reproductive success.

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