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To Chuck or Not to Chuck? Túngara Frogs & Evolutionary Responses to the Puzzle of Natural Beauty

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ABSTRACT. What explains the generation of such beautiful natural phenomena as the dances and songs of birds, the iridescent colours of the hummingbird, the twisted horns of the kudu antelope, and the convolutions of mollusk shells? What explains this seeming gratuitousness and variety of beautiful natural forms? This is the puzzle of natural beauty. Evolutionary responses to the puzzle include the Darwin-Prum sexual selection response and the Wallace-Zahavi honest signaling response. I intend neither to weigh the respective merits of the Darwin-Prum and Wallace-Zahavi responses nor to assess the fruitfulness of extending these evolutionary responses to include both the production and preference of beautiful ornaments in nature and the human practices of producing and preferring beautiful objects. Rather, my intention is to critically assess these evolutionary responses to the puzzle of natural beauty, with a particular focus on the courtship displays of the túngara frog.

What explains the generation of such beautiful natural phenomena as the dances and songs of birds, the iridescent colours of the hummingbird, the twisted horns of the kudu antelope, and the convolutions of mollusk shells? What explains this seeming gratuitousness and variety of beautiful natural

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forms? This is the puzzle of natural beauty. Evolutionary responses to the puzzle include the following:

> (1) The Darwin-Prum *sexual selection* response: sexual selection implies that the more attractive individuals are preferred by the opposite sex, there is an exercise of female choice in mating, and a taste for a particular trait by prospective mates may result in that trait being preserved or enhanced (Darwin, 1871).[2] In addition, it may be appropriate to speak of artworlds in nature, whose participants are involved in a process of aesthetic expression, evaluation, judgment, and change (Prum, 2013, Wilson, 2016);
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> (2) The Wallace-Zahavi *honest signaling* response: the beautiful or ornamented appearance is taken to be a sign of underlying health and vigour (Wallace, 1889).[3] In addition, it may be appropriate to speak of the beautiful or ornamented appearance as a costly display

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[2] Sexual selection, favouring beauty, may be distinguished from natural selection, which favours such traits as efficient metabolism, strength, cunning, speed, and other survival-related traits. Ronald Fisher (1930) has independently confirmed Darwin's supposition that a heritable trait with no positive correlation to male viability may become exaggerated and widespread.

[3] In certain crucial aspects, the Wallace-Zahavi *honest signaling* response is anti-Darwinian: Wallace held that sexual selection is implausible, since natural selection is too harsh and rigorous a process to allow for the frivolity of aesthetic preferences. It also stands opposed to the tradition according to which organisms cheat and manipulate when they communicate (Krebs & Dawkins, 1984).

> that attracts in accordance with the handicap principle (Zahavi, 1975, Miller, 2000, Dutton, 2009).[4]

I intend neither to weigh the respective merits of the Darwin-Prum and Wallace-Zahavi responses nor to assess the fruitfulness of extending these evolutionary responses to include both the production and preference of beautiful ornaments in nature and the human practices of producing and preferring beautiful objects. Rather, my intention is to critically assess these evolutionary responses to the puzzle of natural beauty, with a particular focus on the courtship displays of the túngara frog.[5] Male túngara frogs gather at night in shallow ponds, call to attract females, and compete with other túngara males in these displays. The calls of the male túngara frog vary from the simple to the complex: a whine is necessary and sufficient to attract the female, but chucks make the call even more attractive. To make each mating call more complex, the túngara male may incorporate several chucks for each whine. Furthermore, as each male túngara calls from the water's surface, the body movement creates surface waves or ripples that provide a tactile component to the acoustic and visual components of the

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[4] The governing idea is that traits that are sexually selected for signal that the organism in question has surplus resources that it can squander. According to the handicap principle, beauty can even compensate for certain (genetic) weaknesses that hinder viability. In the human context, the handicap principle explains why artists past their prime reproductive years can still attract young mates.

[5] My account of the courtship displays of the túngara frog will be drawn largely from Halfwerk *et al* (2014). Formerly known as *Physalaemus pustulosus* and now known as *Engystomops pustulosus*, the túngara frog is an amphibian that is native to central America.

courting displays. At the same time, the frog-eating bat (*Trachops cirrhosus*), a predator of the male túngara, can eavesdrop on the acoustic component of the male túngara's call, and the male túngara might stop calling to reduce predation risk and in response to predator cues.

Defenders of the Darwin-Prum *sexual selection* response could maintain that the male túngara must produce a courtship display that is sufficiently attractive in order to secure a female mate. The more attractive mating calls (with up to seven chucks for each whine) are preferred by the opposite sex, there is an exercise of female choice in mating, and a taste for a particular trait by prospective mates may result in that trait being preserved or enhanced. There is the biotic artworld of which Prum (2013) speaks, whose participants are involved in a process of aesthetic expression, evaluation, judgment, and change. The intended audience is the túngara female, whose preference is for complex calls rather than simple ones. However, both predators (such as the frog-eating bat) and parasites (such as the blood-sucking fly) are eavesdroppers that likewise prefer complex calls to simple ones (Page & Bernal, 2006). In the final analysis, this simply demonstrates the classic conflict between sexual selection and natural selection and no recourse is required to either the *honest signaling* response or the handicap principle.

Conversely, defenders of the Wallace-Zahavi *honest signaling* response could adopt the following line of reasoning. Since chucks of a lower frequency are preferred, it will be pointed out that lower frequency mating calls are found in larger-sized male túngaras, which in turn correlate with higher fertility rates. Complex calls in which several chucks are incorporated are preferred by the females, not because they are acoustically attractive, but rather because they are a sign of underlying health and vigour. Furthermore and in accordance with the handicap principle, the male túngaras are demonstrating their willingness to engage in costly displays. In the case of the male túngara, adding chucks could force males into competition with other túngara males and it is only a male that successfully avoids predation by frog-eating bats despite disclosing its location by its costly display that will attract the female (Zahavi & Zahavi, 1997). There is an analogy to be drawn here between the male túngara's courtship display and the peacock's tail, which is otherwise costly and wasteful from a natural selection point of view. The peacock's tail requires resources to build and maintain, attracts the attention of predators, and hinders the ability of the peacock to escape by restricting its flight. Whereas defenders of the Darwin-Prum *sexual selection* response will claim that the peacock's tail has been sexually selected for because peahens find it attractive, defenders of the Wallace-Zahavi *honest signaling* response will claim that as the peacock's tail is a wasteful burden, only males of a certain level of health and vigour can afford such a burden (Al-Shawaf & Lewis, 2017). For the male túngara as for the peacock, the handicap is an *honest signal* that the organism is of sufficient quality to tolerate the burden that the handicap places on it.

This is all well and good, except that it remains to be determined whether the courtship displays of the túngara frog count as an instance of natural beauty. I can agree that there is a variety and seeming gratuitousness of natural forms (mating calls without chucks and mating calls with chucks). However, I think that I am well within my means to disagree that these courtship displays are beautiful. After all, these courtship displays are elaborate and multisensory, involving a visual component (the male túngaras with their conspicuously inflating and deflating vocal sacs), a tactile component (the ripples or water-borne vibrations that reach the female túngara), and an acoustic component (the mating call itself). Emily Brady (2010) provides as an example of natural ugliness the toad, whose face may be judged ugly relative to some norm of human facial beauty. The túngara frog (whose name in Spanish is '*sapito de pustulas*' means 'pustulated toadlet') certainly qualifies as an example of natural ugliness, on the grounds identified by Brady. Even if it is granted that the tactile and acoustic components of these courtship displays have some compensating positive aesthetic qualities, it is conceivable that the overall aesthetic value of these multisensory displays is negative. One might appeal to the familiarity effect: the more familiar we become with and the more time we spend with the túngara frog, the less ugly it will seem to us. However, I find neither the visual appearance of the túngara frog (with its conspicuous vocal sac) nor the acoustic component of the mating call attractive or agreeable, and no amount of familiarity will lead to any positive redemption on the aesthetic front. Indeed, I am in complete agreement with Budd (2000, p. 149) that a grossly malformed living thing (as I take the túngara frog to be) will remain grotesque, no matter how comprehensible science renders their malformation.

One might appeal to the order and harmony of the overall ecosystem of which the túngara frog is a part: while there might be nothing beautiful in particular about the courtship displays of the male túngara, there is a certain beauty that arises when we consider these displays as a key part of a successful, healthy functioning of an ecosystem. This argument is made by Holmes Rolston (1988, p. 241) in the context of a rotting elk carcass that is teeming with maggots: the ugliness does not subtract from but rather enriches the whole and it is contained, overcome, and integrates into positive overall aesthetic value. There is natural beauty in the túngara frog's display in the context of the ecosystem and there is still therefore a puzzle of natural beauty to be explained. I would certainly rank my aesthetic distaste for túngara frogs as on a par with my aesthetic distaste for a rotting elk carcass that is teeming with maggots. Unlike Rolston, however, I do not believe that the appeal to the ecosystem settles the problem of local ugliness and repulsiveness in nature. After all, both predators (such as the frog-eating bat) and parasites (such as the blood-sucking fly) are a part of this ecosystem, foreshadowing the fact of suffering, death, and killing in the ecosystem of the túngara frog.[6]

One might hold that with increased familiarity and more attuned aesthetic sensibilities, an ideal observer would hold that these multisensory displays (with their visual, tactile, and acoustic components) yield an overall aesthetic value that is positive. This could logically be the case from the human perspective of the ideal observer, but we have no understanding of how, from the non-human perspective of the female túngara, the tactile component of the water ripples integrates with the acoustic component of the call and the visual component of the male túngara's inflating and deflating vocal sac. The first problem with evolutionary responses to the puzzle of natural beauty is that they seem to over-generate explanations. Notwithstanding that we are on phenomenologically thin ice with the female

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[6] I am as unsure as Budd (2000, p. 151) is about how the essence of the ecosystem is supposed to guarantee positive overall aesthetic value and natural beauty, despite the best intentions of Rolston.

túngara and lack complete information about how the multisensory components are integrated, evolutionary theorists are swift to draw their conclusions to the effect either that (i) the overall aesthetic value is positive or that (ii) the costly display attracts the female túngara in accordance with the handicap principle. These evolutionary responses can generate explanations for the dances and songs of birds, the iridescent colours of the hummingbird, the twisted horns of the kudu antelope, and the convolutions of mollusk shells (all of which I might hold to be instances of natural beauty). At the same time, these evolutionary responses can equally generate explanations for the courtship displays of the túngara frog (which I hold to be an instance of natural ugliness).

The second problem with these evolutionary responses to the puzzle of natural beauty is (paradoxically) that they seem to under-generate explanations. Recall that the body movement of the male túngara creates surface waves or ripples that provide a tactile component. If it is held in addition that the ripples provide a visual component in the multisensory display, I might differ in my final assessment of the overall aesthetic value of the male túngara's display. After all, I have a taste for ripples that are borne along a water-surface. Were these ripples to be formed independently by a gentle evening breeze playing over the shallow ponds, the morning after the nocturnal túngara displays, I would count the visual scene to be an instance of natural beauty. Evolutionary responses, however, cannot explain the beauty that we find in non-biological natural elements (viz. water-features) and in non-biological natural elements interacting with other non-biological natural elements (viz. wind, water-features), given their biological emphasis on sexual selection, mate choice, honest signaling, and the handicap principle.

The third problem with these evolutionary responses to the puzzle of natural beauty is what I term the beauty-agreeableness gap. Certain traits and ornamented appearances, it is claimed, are preserved or enhanced because they are agreeable to prospective mates, whether as stimuli that trigger certain sensory biases (as in the Darwin-Prum *sexual selection* response) or as honest advertisements of underlying health and vigour (as in the Wallace-Zahavi *honest signaling* response). In the Darwin-Prum *sexual selection* response, agreeable traits are traits that have been singled out by the choosing sex, endowed with an aesthetic sense or faculty. In the more utilitarian Wallace-Zahavi *honest signaling* alternative, on the other hand, agreeable traits are traits that are useful to their bearer and advantageous to the general fitness of the trait-bearing organism.[7] Immanuel Kant, who in his *Critique of Judgment* (1790, §58) identified the puzzle of natural beauty, defends the view that judgments of beauty are intersubjective and have both a social and a cultural aspect. Given the socio-cultural aspect of judgments of beauty, Kant is given to conclude that only human beings are capable of appreciating beauty. I agree with Kant that certain species-specific norms separate the appreciation and evaluation of beauty from the apprehension of mere agreeableness. The peacock’s tail is agreeable to the peahen, whereas it is more than merely agreeable to us human beings who possess the concept of beauty. On behalf of the Darwin-Prum *sexual selection* response, Wilson (2016) attempts to develop an account of sensory bias, according to which human nervous systems must have enough in common with the

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[7] Hoquet & Levandowsky (2015) have reasonable grounds therefore to conclude that the utilitarian Wallace-Zahavi approach resolves sexual selection into natural selection.

nervous systems of non-human animals, that certain formations (e.g. symmetrical and fractal structures) are both easy for nature to produce and easy for animals to develop a taste for. Given the shared physiological basis for our sensory biases, the origins of the human taste for beauty may be located in animals. Such an account, however, does not dispose of the beauty-agreeableness gap. Why are the peacock's tail and the male túngara's courtship displays agreeable to their prospective mates, whereas the former is adjudged beautiful and the latter ugly? Furthermore, if there is a socio-cultural component to beauty, then will not any evolutionary response to the puzzle of natural beauty be necessarily incomplete?

Given these problems with evolutionary responses to the puzzle of natural beauty, a number of issues remain to be properly addressed. In the first instance, one has to define the scope of natural beauty: are we talking about beauty in nature as a whole, the biosphere, the ecosystem, kinds of natural things, instances of natural things, or even natural events?[8] If non-biological natural elements have to be excluded from the scope of natural beauty (as I suspect that they must, given the biological thrust of these evolutionary responses), then the appropriate justification for this exclusion would have to be afforded.[9] In the second instance, one has to determine

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[8] The same question of scope is raised by Budd (2000) in the context of the positive aesthetics thesis.

[9] Ambitious attempts have been made by evolutionary theorists to extend the scope of natural beauty to non-biological natural elements. According to the savanna hypothesis, human beings have a generalized bias toward savanna-like environments (moderate to large open spaces, the presence of scattered trees, smooth ground surfaces, and grassy vegetation of uniform length), since they resemble the Environment of Evolutionary Adaptedness (or

how natural beauty is framed: how do we determine the boundaries of natural things or events that are then subject to judgments and evaluations of beauty? Whereas works of art are discrete and physically bounded (think of the physical frame of a painting and the stipulated length of a musical piece in the concert program notes), what we select as our unit of evaluation in nature seems arbitrary (Zangwill, 2001).[10] In the third instance, one has to concede that not all things or events in nature, even when they are within the scope and the relevant frame of consideration, are beautiful. This amounts to a rejection of the positive aesthetics thesis, according to which all the natural world and its constituents are beautiful.[11]

As I have argued, the courtship display of the male túngara, while agreeable to prospective mates and perfectly explicable by the Darwin-Prum *sexual selection* or the Wallace-Zahavi *honest signaling* accounts, is in my estimation an instance of natural ugliness rather than natural beauty. This ugliness derives from the visual component of the conspicuously inflating and deflating vocal sac of the male túngara, which may be judged ugly relative to some norm of human beauty. Marcia Eaton (2005, p. 48) has elsewhere provided as an example of natural ugliness the pen shell, which is universally described in shell guidebooks as unattractive and assiduously

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EEA) (Orians & Heerwagen, 1992). For a critical assessment of the savanna hypothesis, see Joye & De Block (2011).

[10] This is known as the frame problem in philosophical aesthetics.

[11] *cf.* Carlson's (2000, p. 73) claim that the untouched natural environment has 'mainly positive aesthetic qualities; it is, for example, graceful, delicate, intense, unified, and orderly, rather than bland, dull, insipid, incoherent, and chaotic'. The strongest version of the positive aesthetics thesis has been defended by Hargrove (1989, p. 177), according to whom nature is beautiful and does not contain any negative aesthetic qualities.

avoided by shell collectors. How might the evolutionary theorist account for these instances of natural ugliness? All things considered, once the positive aesthetics thesis is dropped, we are given to acknowledge that what we encounter in nature are not straightforward instances of beauty but rather instances of aesthetic complexity. While many biotic kinds (flowers, the dances, songs, and feathering of birds) are undoubtedly beautiful, other biotic kinds such as the courtly displays of the túngara frog are aesthetically more complex. There is such a variety and a diversity that is exhibited by natural forms that it would be dangerous to reduce our aesthetic considerations of natural forms to the puzzle of natural beauty. If evolutionary theorists finally come to admit that it is aesthetic complexity in nature rather than natural beauty that they are after, then their account remains incomplete as it stands. As I doubt that the beauty-agreeableness gap can be closed without any recourse to a cultural explanation, I remain highly skeptical that evolutionary responses will be successful on their own.

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