The Biological Roots of Aesthetics and Art

Bernd Heinrich, Department of Biology, University of Vermont, Burlington, VT, USA. Email: bheinric@umv.edu.

Abstract: Animals’ choice behavior is driven by motivation that is attributable to both innate urges and from positive and negative reinforcements. Using a comparative approach as well as experimental evidence, I explore how the first involves fitness-enhancing benefits from aesthetics that are derived from ancestral choices via natural selection. Innate urges and aesthetics help guide animals to produce appropriate positive and negative choices that are species-specific. Choices of food, habitat and mates or associates are considered. I propose that art is not a uniquely human product, but a representation or an extension of the maker, as are the ornaments, displays, and songs of a bird.

Keywords: aesthetics, biological roots, behavior, art, animals

Introduction

We pride ourselves as a unique species having a sense of aesthetics that allows us to appreciate the beautiful and distinguish it from the ugly. We suppose that since this capacity demands refined mental traits, it is a subjective topic that is inaccessible to scientific analysis. Unfortunately, such a perspective precludes gaining an understanding of the roots of possibly one of our more defining characteristics, one that has implications for our art, culture and civilization.

Aesthetics concerns our sense of what is beautiful. But what is beauty? It has been variously described as the sole propriety of a beholder, and being skin-deep on the one hand as well as “the substance of God” on the other. Beauty is also the harmonious relationship of facts, ideas and lines and color combinations that make a picture, story or theory out of chaos, which by our sense of aesthetics, approaches what some define as “truth.” Godfrey Hardy (1877-1947) applied truth to mathematics, where the beauty in formulas is “as harmonic as color and words.” What wasn’t true, wasn’t beautiful. To the physicist Paul Dirac (1937-1984) beauty was truth, as when he quipped: “It is more important that the formulas are beautiful, than that the experiments fit.” But truth makes beauty, not the other way round, as the biologist Thomas Huxley (1825-1895) notes in his famous epigram: “Many a beautiful theory is felled by an ugly fact.” Facts are often
unpleasant but they are never ugly, and they can be used to create beauty. But the underlying principle of beauty is still relationships, either of facts, bits of sound, paint, or any other matter, to those to whom such truth is revealed. And to make or reveal that “truth” requires observation, experiment, knowledge, deduction, and craft, all of which may transcend ugly appearance and make beauty. Our aesthetics sense that allows us to valuate the beautiful and parse it from ugly, is like sensations of pleasure and pain that are useful for drawing attention to basic relevancies of life.

Aesthetics, like other sensations, is a valuation of “reality/truth” that concerns many animals other than ourselves. We can deduce its antecedents and decipher how and why specific aspects of it were shaped and developed. My approach, therefore, will be comparative because if aesthetics has a biological function that helps generate appropriate behavior relating to feeding, breeding, and finding suitable associates and homes, then it would be generally adaptive and species-specific.

Aesthetics proximally relate to feelings, but to be examined objectively, we must evaluate it by choice behavior and comparative biology. Attraction and approach versus withdrawal and avoidance are based on sensory stimuli that may be direct, or they may be evaluated symbolically; a cat set onto a picture of three-dimensional perspective will hesitate to cross an edge on it, sensing depth – but by a symbolic representation of the real environment. We do not need to feel the effect of jumping off a cliff to avoid doing it. We also have fear of heights. Judgments are influenced by our senses, but most if not all animals are born with innate abilities to make appropriate decisions of many sorts that affect their welfare on the basis of stimuli that are symbolic indicators, and they are motivated by urges generated by them.

Aesthetics

Recent definitions of aesthetics, upon which “fine” (as opposed to functional) art is based, are diffuse. Scharfstein (2009) defines aesthetics as “anything in experience that is other than the merely literal or practical.” But he then states that “the aesthetic and literal or practical I distinguish are inseparable, except verbally or imaginatively, from the acts, events, objects, or persons of what they are, in the terminology I suggest, aspects or dimensions.” He proposes that the aesthetic dimensions of experience “is the free interest we take in our acts, our thoughts, and in the functioning of our senses. It is the mode of conscious experience, even when the consciousness is evasive and marginal—”. Furthermore, he makes reference to enjoyment when proposing “the seeing is most evidently aesthetic when it is colored with some exultation.” I have gone into some detail in the definition of aesthetics by a current artist and philosopher not because it is made with reference to humans, but because I think it could encompass what a biologist could accept for the experience and productions of animals other than ourselves. The caveat is, though, that one incorporates the evolutionary perspective, where both our own and other animals’ experiences are felt, and acts executed, on the basis of “other than the merely literal and practical.” All are colored by “exultation” or emotion, the proximate mechanism of choice/action.

Other animals’ actions are arguably even less consciously performed for practical effect than ours. They are performed by motivation of what “feels right.” It is only we who
have figured out why they may feel right (or not), because we have deciphered many of the
effects that the animals themselves are not likely to be consciously aware of. For that
capacity of knowing about them we required consciousness and so the product, the
scientific insight, that stands as an edifice of the imagination and skill, and that is colored
by some expectation and ultimately exultation, is therefore art as well.

Our aesthetic sense, as opposed to operant conditioning for a reward, is largely
innate. This fact is now tacitly recognized with regard to appreciation for habitat. For
example, in “the prospect of refuge” (Appleton, 1996), we refer to a view such as one
equivalent to from a cave, or under a tree. We prefer landscapes featuring open space, or
those with a clear focal point such as groupings of climbable trees (Kaplan, 1992), paths, or
water, with wildlife (Orians and Heerwagen, 1992). There may be gender differences, with
women having a predisposition toward prospects providing fruit and refuge (Lyons, 1983),
as opposed to those of hunting and exploration for men. The fact that children show
stronger preferences than adults argues for the innateness (i.e., aesthetic) rather than
learned tastes, those influenced by society and other environmental factors (Ball and
Falk, 1982). I argue therefore for a distinction between the innate or “pure” choices as
opposed to the conditioned ones such as those arising from proximally-reinforcing ones
that we define as operant conditioning. Even pigeons can be trained to distinguish what we
(human children) choose as “good” versus “bad” paintings (Watanabe, 2010) on the basis
of the whole composition of the pictures, and not just isolated parts of it (Watanabe, 2011).
Thus, whereas we are expressing an aesthetic sense, the pigeons’ amazingly sophisticated
discrimination is not the result of aesthetics, but instead from operant conditioning. The
children’s choices were aesthetic. It may be doubtful if children can articulate why they
find specific artistic creations beautiful and others not, any more than birds do.

Aesthetic creations

Birds routinely make judgments that are expressed in their creations. The Great
crested flycatcher, *Myiarchus crinitus*, usually adds a shed snake-skin to the lining of its
nest. Tree swallows, *Tachycineta bicolor*, go to apparent great lengths to gather specifically
large white plume-like feathers for that purpose, and the Red-eyed vireo, *Vireo olivaceus*,
adds the paper from hornet nests to the outside of its nest. Do they have an aesthetic sense?

Birds’ carrying specific items to their nest and incorporating them into it are
expressing a psychological urge. If applied to us, it would signify “aesthetic” appreciation,
but probably only if we were unable to explain the taste in terms of utility, such as pasting
the walls of our home with a flower design. We would say because it is beautiful.
“Beauty,” we presume, is for its own sake, but if art is an expression of aesthetics, then
objectively it must include the creations of animals other than our own. A difference in the
comparison between the birds and us is that we probably know more about the birds’
choices than our own, because our behavior is strongly based by conscious intentions,
especially with regard to what we make.

Animals make a variety of structures from the simple to the highly elaborate, but all
serve a practical purpose. Those of spiders serve as traps. Those of the social insects and of
birds are dwellings, nurseries for the young, or both, and one might suppose that, except for
the constraint of building material, bird nests could or should be alike. Yet, although
between individuals of the same species they vary little, these creations can vary widely even between closely related species. Black-throated blue warblers, *Dendroica caerulenscens*, build their nest within a foot of the ground, and preferably sheltered just under its broad leaves in the fork of a hobblebush. They line this nest with dark hair-like rootlets from ferns that look like moose hair, or as an ersatz when such hair is not available. Yellow-rumped warblers, *D. coronata*, build their nests of thin twigs high in the branches of a large conifer, and line them with dark feathers. The Northern parula warbler, *Setophaga americana*, has a hanging nest built into fibrous lichens. Each of the over 50 warbler species has its own unique places where it builds its nest and with what it is constructed from and in. Some birds literally weave nests using string-like fibers, while a variety of species make pot-like structures of mud and clay and then line them plant down (Goodfellow, 2011). No bird needs to know the deep reasons why it chooses specific nest sites, nest materials and construction techniques any more than a monkey knows why it likes sex (and specifically with a member of the opposite sex of its own species at certain times). Each species has innate “templates” that help identify the appropriate stimuli and execute often highly specific behaviors.

Some likes and dislikes of birds are logically consistent in terms of adaptive scenarios that can be tested. The vireos’ exterior of hornet nest paper decoration (Heinrich, 2010), for example, could be mimicking a hornet nest and thus reduce predation. The large white feathers that tree swallows bring into their nest would hide their white eggs, and could be an adaptive trait reducing chick mortality (During the week of egg-laying, before incubation starts, females other than the nest owner who have not been able to find a nest hole of their own attempt to dump their eggs in others’ nests, and for this egg-dumping tactic to succeed a prospective cuckold needs to make sure the potential host is in the process of completing its clutch. That is, it may need to see the others’ eggs. So the preference for white feathers translates to good parenting, because, in nests with extra young, some of the young do not survive to fledge because, in this species, individual young can dominate siblings by plugging the nest-hole entrance and intercepting most of the incoming food (Heinrich, unpublished). In contrast, some hawks daily add fresh greens into their nest lining, but only after their young hatch when the parents stockpile meat in the nest (Lyons, Titus, and Mosher, 1986). A dead hare may spoil long before it is entirely consumed, and it would then contaminate the nest lining for the next meal. The greens may be providing a “clean tablecloth” that retards food spoilage (Heinrich, 2013). Whether birds themselves consciously know why they have the specific tastes is probably irrelevant in their decision-making process, because the evolutionary “reason” to get it right would require an in-depth understanding of advanced PhD level biology, and would even then be highly convoluted and too complex to fathom. It is simpler and more reliable to simply program tastes. Similarly, what our “eye” relates to us as appealing may also be as unknown to us as the urge to collect white feathers is to a tree swallow and the penchant to collect green boughs is to the Broad-winged hawk. Our tastes for different kinds of food, on the other hand, are (in the last century at least) becoming more transparent, and therefore we are less apt to think of them as “aesthetic” since we now also consider health effects.
Food choice

Animals proximally judge the proper food to eat by taste. Taste preferences are largely innate, as are some cues that identify food, such as color, shape, and scent. Honeybees are attracted to gather sugar from flowers on the basis of their scents, colors and geometrical patterns (von Frisch, 1954). We do not need to suppose that they find flowers “beautiful.” Aesthetics could be irrelevant, because these insects are strongly conditioned by the food rewards, whereas we pick the flowers simply (or more complexly!) because we consider them “beautiful” and therefore worthy of being grown in a garden or displayed in a vase on the table. Yet, the dichotomy between innate attraction and conditioning is not strict since bees would likely have difficulty in finding flowers if they did not have an innate attraction to the specific general stimuli that represent generic flowers. Secondly, their chances of finding nectar are increased also by specific innate choice, because blue flowers on average have more nectar than white flowers. (Bird-flowers tend to be red, bee flowers blue, and fly flowers white). Honeybees, *Apis mellifera*, (Menzel and Erber, 1972) and bumblebees, *Bombus* sp. (Heinrich, Mudge, and Deringis, 1977) indeed have a stronger innate attraction to blue rather than white flowers, and bumblebees also have an innate preference for flowers with bilateral symmetry (Rodriguez, Gumbert, Hempel de Ibarro, Kunze, and Giurfa, 2004), which should reduce chance visits to random objects. Bees’ senses of being attracted to flowers in general, and specifically to being biased toward blue and bilaterally symmetrical flowers, are arguably aesthetic if referenced to our tastes, so why should they not be aesthetic if referenced to theirs, provided the individuals’ choices were not preconditioned on their experience creating an expectation of reward?

Insects’ behavior may, however, seem to be unjustified in terms of aesthetics simply because we associate that faculty with “intelligence.” Some vertebrate animals, on the other hand, exhibit choice behavior that, because of its detailed discrimination based on generalized features, is difficult to reduce to discrete “mindless” qualities such as color or scent. Both Black-capped chickadees, *Poecile atricapillus* (Heinrich and Collins, 1983) and Blue jays, *Cyanocitta cristata* (Real, Ianuzzi, Kamil, and Heinrich, 1984), for example, have been taught to distinguish the differences in the shapes of leaves that are undamaged, partially-eaten by palatable caterpillars, or partially-eaten by unpalatable caterpillars. Similarly, Rock pigeons, *Columba livia*, can discriminate features in pictures that relate to human aesthetic value (Watanabe, 2010, 2011). The birds’ ability to generalize features – in the first case with regard to forms, in the second of colors and patterns that relate to human aesthetic sense – is impressive. In the above cases, however, the preferences cannot be regarded as aesthetic because the choice behavior was not spontaneous. It had been shaped by rewards and is presumably motivated by those rewards. On the other hand, relatively naïve monkeys do have spontaneous preferences for visual stimuli similar to those that naïve humans find pleasing as well, and this has qualified them as being “aestheticists” (Anderson, Kuwahata, Kuroshima, Leighty, and Fujita, 2005; Rensch, 1957).

If, for some reason, presumably mindless creatures cannot be considered aestheticists, then consider an animal of considerable acumen (Heinrich, 1995a), the Common raven, *Corvus corax*. Like many insects, it also has visual templates that serve the young inexperienced individuals. Naïve young ravens are attracted to bright-colored and
shiny objects, such as rings, coins, gems, etc., that appear to have no utilitarian value (Heinrich, 1995b). The naïve birds are also attracted to round, as opposed to elongated, objects (Heinrich, Marzluff, and Adams, 1996). Furthermore, young inexperienced birds are curious but highly cautious of large furred and feathered objects. The predispositions of naïve birds to be attracted to these stimuli have ultimate (i.e., evolutionary) biological significance, because they represent foods, such as insects, fruits and eggs, as well as carcasses. The latter, however, may be confused with a live sleeping predator, and therefore require caution to approach. The caution by naïve young birds is like an innate “knowledge” of potential danger that, like some peoples’ fear of snakes and spiders, predetermines choice-behavior and then can modify the behavior by learning.

Primates eat fruit, which have evolved to stand out from green foliage by their colors, as do flowers that attract pollinating insects. Given that the plants coevolved with their animal pollinators and seed dispersers who have both evolved tri-chromatic color vision, it is predictable that these animals would also have evolved the behavioral attraction to color and/or color contrasts. Their neophilia is a learning predisposition that draws attention to their food in a background of green foliage to then promote appropriate behavior.

Food may be initially located by vision and scent, but it is evaluated by the eating. Hence, chemicals relevant to food identification, as detected by chemical receptors, must be linked to the central nervous system to be valued depending on its suitability as nutrition; the animal cannot logically deduce their health effects. For the most part it must “know” whether food is nutritious or harmful. Aesthetics can serve as the first filter. Indeed, for some people, the taste of food has been elevated to make “dining” and cooking an aesthetic, if not an art, experience. It is no accident that our perception of “good cooking” is often related to “simple” and healthful food, and that the old masters invariably chose ripe fruit as their models, rather than the achronamic, shriveled, rotten, or green. Nevertheless, food choice is broad and easily alterable. In contrast, in sexual attractions, which are similarly guided by specific innate preferences/tastes that relate to scent, vision, and other senses, choice is strongly hard-wired and relatively unalterable.

Choice of Mates and Associates

Innate choices triggered by specific sign stimuli are important for reproduction in all animals. Mating may require highly specific rules, and the ornaments and behaviors to achieve it can be costly, as shown, for example, by tail ornaments in birds.

A birds’ tail is normally used as an organ for steering and/or flight, and if potential mates choose a mate proximately on the basis of the appearance of its tail, and ultimately on its utility, then an aerodynamically perfect tail might result. But the peacock’s tail (and those of some others as well) is useless as such. It is large enough to be a physical burden to produce and to carry around, and brightly-colored enough to bring the wearer to the attention of predators. However, as pointed out by the theoretical biologist Amotz Zahavi (1975), it gains its impressiveness primarily for its cost (if it were cheap to produce and wear than each male could have one). The price a male peacock pays in essence shows that he is alive and well despite wearing his long colorful tail that could cost him his life. But to mate he must wear one that meets specific expectations, because the females’ aesthetic
sense is cued to choose that specific ornament.

Appearance identifies quality, and the first aspect of quality for a potential mate is to identify the proper species to choose, and the next is the choice between individuals. The nuptial sky dance of the male woodcock will never impress the hen of a grouse or a peacock. Yet, in a more fundamental way, it boils down to the same thing in all species. Whether it is the red buttocks of a baboon, or the brilliant flashing green head and neck of a mallard duck, the huge rack of a stag, or the shapely breasts, hips and long hair of a young woman and how they are displayed, it’s all about aesthetic taste. And that taste, like all tastes, has meaning in terms of signaling desirable qualities relating to reproduction of the individual bearing them, or of an individual as an ally in the more social animals.

Most birds offer themselves in body, by their dance and song, in their skill in construction, and ability and competence to offer help to a potential mate. All of the potential attributes can be incorporated into ritual displays that attract mates where specifics and subtle cues matter. The individuals in a group of displaying male sage grouse or birds-of-paradise may all look and act alike to us, but the potential mates who watch them and judge are highly selective, and there is usually a near consensus among them as to which one is the most attractive of them all in the line-up. The animals are acutely aware of specific cuing signals, but it would be hard to argue that they consciously know why they prefer them. Appearance and behavior may reflect hormone levels and physical conditions (Ligon, Thornhill, Zuk, and Johnson, 1990). One may perhaps debate whether such fine-tuned taste is “aesthetic” (Thornhill, 2003) or whether it includes art (Endler, 2012), though there is no doubt about its effects and relevance, and that the choices could generally not come from operant conditioning.

There is, for humans, such little ambiguity about the general body features that do or do not signal reproductive potential that is translatable to physical beauty, that a discussion of them in the present context is superfluous. On the other hand, the face is as important, yet few of us can articulate what we see that makes a face beautiful. But not all cues need to be consciously evaluated, nor do we, as in birds or other animals, need to be aware of them for them to affect choice behavior. Again, consider other animals for whom we do not suppose that they consciously know what attracts them. We call it “instinct,” and if applied to us we might say “impulse” or a “heeding of the gut.” But if it is an evolved aesthetic enabling us to act on the instinctual knowledge that we have acquired over our history, then it is so firmly grounded that it is no longer necessary for us to be conscious of it. Consciousness could delay and divert from what has produced the proper result through evolutionary history. It may, however, help to be consciously aware if one wanted to reproduce the cues symbolically, and I suspect an artist has the ability to bring instinctive attractions into expression, which is referred to as having a “good eye.”

The “eye” can be tested, and one of the (to us) unconscious features of facial beauty that has been revealed by experiment is something none of us would likely have articulated; namely, symmetry (Brown et al., 2008; Little and Jones, 2003; Samuels, Butterworth, Roberts, Grauper, and Hole, 1994; Thornhill and Moller, 1998). Physical symmetry has now been extensively examined not only with regard to facial features in humans but also in respect to other bodily features in insects, fish, birds, etc. (see references in recent article by Langridge (2006), on a mollusk, the cuttlefish). Is it an averageness that helps to identify the relevant features of the type?
We are, apparently, programmed to recognize and be attracted to certain features that are not different in kind than those important to a peacock, widow finch, or a barn swallow, whose females are programmed to be attracted to a male with a long tail feathers. Needless to say, Vargas did not get famous painting models chosen specifically for deformities, disease, or old age. The models were chosen instead by criteria for beauty. Beauty is in the eye of the beholder, but in this case there is relative uniformity in the eyes of the intended beholders, and the artist was privy to it, and also had the skill to paint what his audience wanted and expected.

We also value “inner beauty,” perhaps roughly translated to “spirit,” because we are highly social and our survival as a social species has depended on the wisdom and necessary knowledge of post-reproductive individuals. As a consequence, artists may display “character,” in which case the emphasis is on the face rather than the body. However, almost invariably when artists draw a portrait, there is an attempt to display the positive elements of the subject possibly through the, perhaps, superficially negative elements that may be included to warrant the “truth.” If negative qualities are deliberately displayed, then they are meant to indict an enemy. If conscious, then it would be advertisement or propaganda, as would a reaction to it. Neither would be fine art, regardless of what it is a reaction to or against.

Aesthetic taste is not displayed only on the living body and/or behavior, but also on products the individual makes and is then associated with. For other animals, the best example may be that of the bowerbirds of Australasia (Frith, Frith, and Barnes, 2004). The Satin bowerbird, *Ptilonorhynchus violaceus*, stays at and in the vicinity of his bower for years, daily attending, maintaining and improving it. It is a large construction of two parallel walls of upward-extending twigs that arch upward and over an avenue in a north-south direction (across the sun). It is erected in a carefully-kept clearing a meter long and wide with a smooth floor on which some 50 or more preferably blue berries, parrot feathers, and other shiny trinkets are arranged for prominent display. The birds’ attraction to blue decorations is so strong it may even kill small blue birds for its feathers. In contrast, the Vogelkop gardener bower bird, *Amblyornis inornatus*, builds a bower that is up to 1.6 meters long and over 1.2 meters tall. It resembles an “extremely well-made and neat” conical hut. The bird maintains a meadow of moss free of debris in front of it, and displays on this “lawn” piles of colorful fruit, flower petals, fungi, and insect parts, all arranged according to their different colors as though aiming to provide maximum contrasts between them (see Frith et al., 2004; Goodfellow, 2011, p.143).

**Show of Skill**

Birds’ displays in sexual selection are, aside from feather garb, often exquisite demonstrations of skill. The dances of the South American cotingas (*Cotingidae*) and Australasian birds-of-paradise (*Paradisaeidae*), the nuptial flights of the North American woodcock and the raven, are out of the ordinary or everyday behavior of these birds; they are highly distinctive special displays of perfection through strength, coordination, and ability to measure up to an ideal, as are Vargas’ paintings of nudes with respect to morphology. They are for an audience, and that audience judges them critically. Song is often an accompanying demonstration of skill.
We not only adorn ourselves with clothes, jewelry, body paint and markings, but by extension also by the products of our skills, such as music and other art. The aesthetics of products are generally clearly identified as being a part of the individual.

Birds’ nests are a particularly conspicuous example of sometimes exquisite skill of their creators, but since the designs are highly species-specific (Collias and Collias, 1984; Goodfellow, 2011; Haskell, 2000) and serve a utilitarian function, they cannot generally be regarded as satisfying tastes. However, for some species nests do serve as mate attractants and that then cater to tastes. A presumed outgrowth of nests as display objects are the bowers built by the afore-mentioned male bowerbirds, which are primarily, if not exclusively, for display.

Whether it is the elaborate bower built by a bowerbird (Frith et al., 2004; Goodfellow, 2011) requiring years of practice to achieve, a rock star’s CDs or a painter’s art, all are extensions of the individual. Similarly, if someone shows us a beautiful print of an anonymous painting, we are less impressed and less interested than if we saw who created it, knowing it is the extension of the contents of the persons’ brain and their skilled hand and thus really an extension of him or her.

It is difficult to imagine artistic expression without a heavy dose of skill required to produce the show even in human art. Indeed, often the skill IS the show. A gymnast or skater may be physically fit, but the essence of their projection is skill. Playing a recording of its species-specific song may attract a conspecific bird, but if a show-person came to play to a human audience a recording that happened to sound nice, rather than exhibiting their skill by their own vocalizations and their own skill on the strings or keyboard, we would not be impressed. Skill impresses, and skill is almost by definition that which is superior to what we ourselves can or could do routinely.

Habitat Choice

Animals are adapted to live in specific habitats, but to choose one it must first be able to identify it. Presumably Wood thrushes, *Hylocichla mustelina*, for example, should find dense woods attractive and Savannah sparrows, *Passerculus sandwichensis*, open fields. Birds’ habitat-specificity is presumably derived from visual cues that are symbolic enough to identify some key feature or features of their often fine-grained and specific habitat. Like food and mate preferences, choice for their specific habitat is genetically engrained. But what exactly are the cues for something as difficult to define as “habitat”? We don’t know, but the relevant cues could include sign-markers, such as perhaps open vistas versus closed, irregular patterns such as cover of trees versus an even horizon near the ground, attraction to specific colors or scents, complex pattern versus simple, sunshine versus shade, and perhaps horizontal versus vertical lines. Gulls as seabirds, for example, may be expected to be attracted to water, yet they now also forage on open fields and parking lots, so open space or a horizon may be their relevant attractant cue rather than water as such. Similarly, cliff-nesting peregrine falcons now nest on tall human-made structures, presumably because they identify similar specific cues there that match their innate ones.

Innate human habitat preferences have been expressed and documented in the references to numerous studies by Edward O. Wilson’s books (1984, 2004). We evolved
out on the open plains with scattered trees and may have an innate attraction for park-like vistas, given our attraction to the shelter of trees and prominences. Our fascination with animals is part of the same aesthetic sense, specifically labeled as the “biophilia” hypothesis. We were and are fascinated by animals, as cats are by birds and hounds by hares. A landscape replete with a diversity of animal life is for us a habitat that is suitable for our life. Similarly, one with flowers has a signature of open space, sunshine, and it automatically presupposes productivity, a habitat where there are animals. Thus, it is no wonder that we have an aesthetic sense for color contrasts, one widely exploited by artists, often directly in using flowers as models. But that aesthetic environment includes not only our visual cues but also an aural landscape (Fisher, 1998, Pijanowski et al., 2011).

If the osprey’s aesthetic sense dictates that it must nest on a platform of branches of tall trees, then if we cut down old trees we should (and do now) provide substitutes. Similarly, if our aesthetic senses are a basis for what makes us human, then they inform moral choices. If aesthetic tastes refer to adaptive responses to living in a certain environment, then this suggests that we should make efforts to retain and create environments that we find beautiful and pleasing because our well-being depends on it. Since we are relatively plastic and subject to experience, early contact in childhood (Louv, 2008) may be required to facilitate the innate developmental trajectory.

The innate sensory stimuli that through our evolutionary history have conferred beneficial effects on us may be transferred to our art, perhaps through a “sensory exploitation” (Verpooten and Nellison, 2012), a concept that does not explain the origin of the original preference, but is useful in explaining effects. The visual effects that, perhaps most effectively, match human aesthetics of landscapes with skill enough to be effective may arguably be paintings such as those of Albert Bierstadt, Thomas Cole, and Frederick Edwin Church. With relevance to conservation, recent books argue to save not only the symbolic but also the real (Berleant and Carlson, 2007; Brady, 2003; Budd, 2002).

Art

Art, as Leo Tolstoy (1896, 1996) understood it over a century ago, is: “a means of intercourse between men.” He apparently falsely presumed that only we have the capacity to receive/perceive another’s experience or their expression of feelings. Any dog owner knows otherwise, and the dog is only a single of innumerable species. Many of us are close enough to just this one to know it intimately to some degree.

Eible-Eibesfeldt (1988) acknowledged that human aesthetics refers to what is beautiful and that our sense of it may have a biological basis because of an apparent consistency with regard to brain laterality, whereas beauty as defined by culture instead is nebulous related to “good form.” However, we now generally accept that art expresses human tastes of beauty, pleasure, and skill that are of evolutionary origin related to fitness (Dutton, 2009), and other animal’s tastes are presumably similarly derived, though therefore given different expression in accordance to different needs of life. Yet, we know now that even apes can make paintings (Lenain, 1997; Lestel, 2011; Morris, 1962), which induced one reviewing artist to remark: “They pretty much say it all. I spent years getting a degree in something [making paintings] which monkeys do innately.”

Some would say (Lewis-Williams, 2004) that we didn’t have art until we had
Biological roots of aesthetics and art

consciousness. Thus art, at least anthropocentrically, is a conscious expression of something of our inner nature. But of what? To Scharfstein (2009), art stems from our “hunger or need to create, contemplate, possess… at least a shadow of what we do not have fully enough to satisfy us” so that art becomes a “testimony to the maker’s traits.” It is, as in other animals, indeed an extension beyond the verbal expression, though arguably to an even greater extent than in those who have no verbal expression. Art includes imagination, hunger, skills to explore and make “imagined possibilities less figuratively, more tangibly,” and make them “more accessible.” It is, according to Scharfstein, a “reconnoitering of the worlds’ interesting possibilities and yet avoid the inconvenience or danger of encountering…. I suspect the cave paintings, and those of Hieronymus Bosch (1450-1516), would come to mind as the latter, and those of Leonardo da Vinci in the former.

Some 32,000 years ago, from when we have the earliest recorded human images that have been preserved (on cave walls in Europe), we painted animals, and most likely in ritualistic or shamanic contexts to make them directly relevant to a most important aspect of our reality then: the prey we enjoyed to hunt. They represented our “reality” and hence our “truth.” Our sensory-perceived connections to nature are now not as close as they were then, and so our art now would expectedly also be more symbolic of that past. Joel Babb, an artist who paints (to us humans, not meadowlarks) beautiful pictures of wooded streams and brooks told me: “I don’t know what the deep reasons are behind the interest [in humans] of the beauty of clouds rising behind a ridgeline, or white pine branches reaching in front of a cloud, or a brook coming down through the woods splintering the brilliance of light…. But the interest is there for us.” Billowing clouds and the open sky appeals to our ancient heritage of hunters on the relatively open plains, savannas and open bush-land country such as in Africa, in which we feel even now much more at home than in closed-canopy dark forest. In the open, as hunters, we could spot game, and as the hunted at times also, we had time to climb a tree. So trees represent safety. I suspect further that the hanging pine branch touches an analogue of “frame” such as one would visually experience under a tree, or perhaps a shelter from a cliff.

Babb uses flowing water as a persistent theme in many of his paintings. His brooks and streams look alive, shimmering and moving- the stimuli we associate aesthetically with water. Water represents life to us. As hunters running down an antelope in the heat – the only arena where we gained an advantage over the big cats – access to water was essential. Unlike other open-country animals that must retain water to the utmost, we gained our advantage through copious sweating. Sweating was key to hunting in an open sunny habitat, and those of our ancient ancestors who were near water gained a huge advantage relative to those who lived far from it. Those who had a great attraction for water were likely those who wanted to settle or be near it. We see the evidence of our innate appeal to water in the value of real estate; a cottage at the edge of a lake or stream costs at least double the same one in an open bare field, or in thick woods without a view. If we had evolved to live underground, or on treeless plains, our aesthetic tastes would be very different.

Neophilia and Art

In a (strictly theoretical) unchanging environment, specialization should ideally
become fossilized by hard-wiring to reduce or eliminate wrong choices. Learning can fill in for change, but it may require time, and it necessarily involves exploring something new and making mistakes (which can be minimized by correct insight) before there is correction to achieve appropriate behavior. As already mentioned, food choice is a good example and has been well-studied in insects. After bumblebees have specialized to forage on the “best” of available flowers, and that flower stops blooming or is removed, they become attracted to the new. They sample a great variety of flowers, which enlarges their choice horizon. They then choose the best of those available on the basis of food rewards (Heinrich, 1976). Similarly, although adult ravens are attracted to specific features in mate choice (Gwinner, 1964), the young naïve ravens’ are biased to novelty. They preferentially contact and manipulate the new regardless of food value. After several contacts, however, they ignore all but the edible, which are then hunted preferentially (Heinrich, 1995b). On the other hand, ravens have innate attraction to smooth, round and colorful objects whereas elongate objects are neutral (Heinrich et al., 1996). Such cues indicate what might be edible, namely berries and eggs, and these serve them as a first approximation that shortens or even permits subsequent conditioning, but is not the cause of it.

Humans also value uniqueness as an aesthetic appeal. We pick a bright blue flower out of a field of the red. We, too, are attracted to fruit, to bright colors, and to eggs. However, we exhibit a huge range of individual tastes, in addition to valuing uniqueness. Are the two related? To try to answer that question it is perhaps appropriate to first acknowledge that we are, more than any other, a species in which learning assumes an overwhelming importance. The addition of conditioning onto the innate predispositions results in us having a large variety of tastes. My own view is that, until shown otherwise, we are unique quantitatively, but not qualitatively. Again referring to bumblebees, there is so far no evidence that their innate attraction to flowers vary to any significant extent, but preferences may vary greatly among the individuals of the same species and even in the same locality. Flower morphologies vary greatly, and the rewards may be nectar, pollen, or both. Harvesting techniques vary greatly as well, depending on what is harvested, and even more depending on from what. The morphologies of the different flowers demand specific behaviors to exploit (Heinrich, 1976, 1979b), and they are identified by specific attractant cues. The results of individual specialization, however, are adequately explained by conditioning (Heinrich et al., 1977). Similarly, Common ravens preferentially nest on cliffs and forage in association with wolves wherever one or both occur. However, their curiosity and flexibility allows them to fill in to contact and then be conditioned to a great variety of options for food, habitat, and nest sites. As a likely consequence these birds may be able to occupy a wider geographical range and wider ecological conditions than any other bird species.

The ravens’, as well as our own, neophilial tendency facilitates staying informed and would also have importance in the ability to spread into new habitats, and hence to achieve world-wide distribution and success in discovering the many possibilities, riches, and opportunities. In bumblebees, it permits the tracking of resources available in different flowers through a season in the same place, as is required in their annual colony cycle (Heinrich, 1979a). Solitary bees, in contrast, which can specialize on specific plant species blooming at any one time, have a narrow preference window and presumably a lower learning capacity.
Attracting signals could be labeled as “aesthetic,” provided they are not based on conditioning, but the experiments with ravens show them to have a utilitarian basis (even when at times it causes them to pick at bottle caps or carry golf balls to the nest). Novelty as an aesthetic sense thus has not only benefits, but can also involve the costs of making mistakes. Translated to art, this tendency means that the “new” catches our eye and so variety and complexity as such may be aesthetic. But if the comparative approach with other animals is indicative, it also means that there are discrete limits to the novel that are beautiful. Making something ugly is not innovation. Style is a different category.

Artists over the centuries painted in distinctive styles. The beauty of the Flemish landscape painting is distinct from the majestic paintings by Albert Bierstadt (1830-1902) of the western North American panoramas. More recent paintings, such as those of Andrew Wyeth (1917-2009) display a readily-recognizable personal stamp, different both from that of his father, N.C. Wyeth, and his son, Jamie. Joel Babb’s paintings of the New England brooks and forests are again a vastly different style. But all are of nature and people and their works. All are innovative, and distinctive. But the one thing that they are distinctive for is aesthetic beauty. It is generally presumed that art is not necessarily representative of anything, and some even say that if it is representative then it is not art! On the other hand is that which does not look like anything to the average person really art? Or is art anything one says it is?

During a recent visit to the Peabody Essex Museum in Salem, Massachusetts, I greatly admired a private collection of Dutch and Flemish master paintings that date from the 1400’s to 400 years later, and thought how it must be a brave person who, after that glorious time of these artists’ achievement, would dare to apply paint from brush to canvas, if they were in need of public recognition to produce something that might be superior to this, in order to stand out enough to make a living. But when I looked at the contemporary paintings on the wall of my hotel, it seemed that I was looking at trash that almost anyone could have produced. But it must appeal to some. How can the difference in appeal from the old to the new be reconciled in terms of aesthetics or do aesthetic tastes change radically over time?

**Alternative Strategies and Post-Modern Art**

Beauty as a commodity is best understood in animals, and in most animals’ mating games “beauty” becomes a commodity in literally head-to-head competition. In the social sphere, the competition is in precise parameters and by “rules” that the contestants follow in order to remain in the game. In balloon flies (Diptera: Empididae) the mating “rules” are that males dance in crowds. They are then chosen by the females out of a line-up on the basis of large empty balloon-like construction of silk that these courting males offer as mating inducements (Kessel, 1955). These “balloons” appear to be useless except as an aesthetic offering. What do they offer these females aside from satisfying their “aesthetic” sense? The answer is “nothing.” However, that “nothing” evolved from something that did have value, but the attraction to it was achieved by hijacking, in what amounts to marketing deception. That story emerges from the likely prior evolutionary steps that can be deduced from some species of the genus *Hilara* in this group.

The original steps to the empty “balloon” attraction involved males who increased
their social success by offering prey that was wrapped in silk, thereby presumably making it easier to handle, and females then evolved to choose males with the largest offerings. Competition among males to carry large prey may have compromised dancing performance, but some males compensated by making their gifts more conspicuous by better “gift-wrapping.” After the females evolved to become attracted to the enhanced, new stimulus for food, it in turn selected males to leave out the contents and carry empty packages, which they could make large to increase show alone, since “real” value was no longer relevant. Could similar principles apply more universally?

As shown by the example of the peacock’s tail, rules of the self-marketing game may be stringent and costly. Many males of a population may not breed. The individuals who don’t measure up to the winning standard do something different than appealing to aesthetics. In some species of insects, fish, birds, and mammals, instead of showing off their finery and competing head-on, some males adopt nondescript garb and manners and so enter into the arena “under the radar,” so to speak.

If art is an expression of aesthetics to create beauty then one might expect marketing it to generate two kinds of strategies. The first concerns utilization of the aesthetics related to the unvarying life-promoting aspects ultimately based on food, safety, comfort, and reproduction. The second is instead with respect to exploiting client relationships in which social aspects are an issue.

Those who paint “pour l’art” are presumably driven by aesthetics, the tastes that are generally widespread because they spring from our biology and are influenced by our expectations from style. However, choice in what has been described as “post-modern” art boils down to two constituents: Name and Number. Two paintings can be identical, and one can demand an astronomical price, and the other be ignored. The difference is that one is by a famous artist and the other is by an unknown; the painting selling for a million dollars would likely be discarded by the same buyer if they were ignorant of its painter.

Aesthetics may be the least of the value of postwar modern art, and perhaps also the content of it, as is prominently displayed in a recent (31 August, 2012) New York Times article by James B. Stewart on a comparison between recent astronomical prices of real estate and art. The article asks: “If its $100 million, is it art?” The premise of that question, that “art is what people are willing to pay,” implies that “an apartment is like a piece of art,” which, as Cezanne’s “The Card Player” that sold for $250 million demonstrates, simply means it is worth a lot of money. If this premise is true, it follows that art is determined not by the object but absurdly either by the amount of available money, fools, or both. Alternately, art is defined as something that is “unique and can’t be replicated.” However, the random splotches of paint thrown onto a wall or canvas by any chimpanzee could never be exactly replicated. Each is unique. It is true also that the portrait of the faintly smiling Lisa Gherardine by Leonardo da Vinci can’t be replicated. But a reasonably technically capable artist could make a close copy, and a blue plastic rectangle that sells as art can probably be replicated by almost anyone. What would be reduced in a replication, though, is not beauty, but the monetary value of the original by threatening their ownership of “one of a kind.” Where value is all about demand, buyers need both assured rarity and Name.

Art is also defined as something without practical use. But the fluted marble columns holding up the roofs of the Greek temples are still beautiful, whereas white-
Biological roots of aesthetics and art

Painted columns created for beauty and set in front of a house built to live in make it look ugly. The designs of a feather, or that of an egg, are highly functional, and beautiful to whomever that design is revealed, but any imaginary construction trying to serve the same function of either is necessarily ugly; it reveals not truth but an individual’s whim.

Ernst Beyeler, the great Swiss art dealer reputedly said: “If I can’t sell something, I just double the price.” If this strategy is effective then it acknowledges the facts that for the seller the high price is meant to let the buyer presume they are buying something of greater value than what they see, and that to the buyer the “something” is not art but money. It’s a confidence scam where the purchase is reduced to money to become a pawn in a financial investment, rather than chosen as a work of craftsmanship and beauty. Donald Kuspit (2004) in “The End of Art” posits that post-modern art is “post aesthetic” and has degenerated into an entropic character. However, especially in its most bizarre examples, post-modern art makes newspaper headlines. These generate discussion and garner even more attention, and so there is even more inducement to go yet another step in the same direction into idiosyncratic and purely personal, which turns out to be a distancing from the broad biological roots of what is innately pleasurable for our species.

We are like other animals except that we are clever and flexible enough to be able to substitute fake for real value. A peacock risks his life to predators to back up his worth with what appears highly attractive to the discriminating intended client. We invest in “something” (which could be anything) that we call art. As the artist Joel Babb, summed up: “It is only the insiders who are educated to the point of not being able to distinguish shit from shinola, or the pulling off of a scam that is working” and “it can’t be good for art or society in the long run- it’s like a virus which infects everything, but it can be amusing.”

A personal note

The above exploration would not be complete without a consideration of personal evolution and possible biases (although if they were strictly personal they would be irrelevant). I rather think of them as general, but that realization came only after exposure through science and art, after which I realized that the effect of collective culture can overwhelm and squelch aesthetic sensibilities as well as hone them.

We are a species that more than any other lives by learning. We absorb at first passively, then actively as we try to “belong” to that which to most of us now means largely the urban environment. I experienced a facilitated exposure to a much different one. It was much like that of some birds who learn their species’ songs by hearing it around them while they are still in the nest. That is their specific learning “window” of time, the only one that song learning by them can occur. Learning occurs only with emotional arousal, and originally that arousal comes from our innate aesthetic roots where the relevant catches our attention.

I recall my intense emotional arousal from animals of all sorts. In part my father facilitated what was likely this natural predisposition, but I soon focused a burning fascination on birds and beetles, possibly because they were the most readily available subjects. I recall also a special romance for marshes, which seemed like a heaven yet unseen but only glimpsed, perhaps from a picture or a verbal description. Pictures of the real thing were evocative because they seemed to touch the same feelings.

Later, as a young man, during a year in the African wilds and months in dense
forest, I experienced exhilaration to be finally out of them and onto the Acacia savanna with views into the distance, with breathing space, birdsong, and animals and their tracks as sign. I knew nothing of the “Savanna hypothesis” or the “Hunting hypothesis.” Thus, I believe my strong biases then were “pure” aesthetics. They emerged from direct exposures and comparisons that allowed weighing one sign stimulus against the other on the emotional scale.

Early on, I wanted to “capture” and keep the beautiful. At first that was literally by hunting, using whatever means I had available: hand, net, slingshot, gun. As a kid I could keep insects. Later I raised young birds as (free) pets, and learned taxidermy to preserve animals. I moved on to photography, and then to sketching and water-coloring. Later still I tried to “capture” deeper non-visual aspects of beauty through science, which led to writing and enlarged the vistas of reality into ever-wider contexts or frames. The large frames of reference were almost like my beloved “marshes,” savannas or other encompassing ecological settings. There was little aesthetic distinction between the beauty of a marsh or an aesthetic intellectual framework that placed the animal or plant into the construct of an ecosystem, or into the time-frame of evolution. But such “realism” never could or needed to be absolute. It could only capture fragments and essences that would isolate, represent, or symbolize the key features that evoke the aboriginal feelings.

We are imbedded in a collective culture changing us in an ever-tighter spiral away from our aboriginal aesthetic roots and into an alien existence. I believe that the closer we live to our aesthetic roots, and the more we are exposed to them especially during our childhoods, the more we will be able to live contented and healthy lives. Art has the power to help bring us closer to that aesthetics, which may be obscured and hidden, but which we need to access in order to feel whole.

Acknowledgements: I thank Joel Babb, Jennifer Vonk, and an anonymous reviewer for thought-provoking suggestions and editorial comments.

Received 06 June 2012; Revision submitted 23 August 2012; Accepted 27 August 2012

References

Anderson, J. R., Kuwahata, H., Kuroshima, H., Leighty, K. A., and Fujita, K. (2005). Are monkeys aestheticists? Rensch (1957) revisited. Journal of Experimental Psychology: Animal Behavior Processes, 31, 71-78.

Appleton, J. (1996). The experience of landscape. New York: Wiley.

Balling, J. D., and Falk, J. H. (1982). Development of visual preferences for natural environments. Environment and Behavior, 1, 5-28

Berleant, A., and Carlson, A. (Eds.) (2007). The aesthetics of the human environments. Toronto, Ontario: Broadview Press.

Brady, E. (2003). Aesthetics of the natural environment. Edinburgh: Edinburgh University Press.

Brown, W. M., Price, M. E., Kang, J., Pound, N., Zhao, Y., and Yu, H. (2008). Fluctuating asymmetry and preferences for sex-typical bodily characteristics. Proceedings of the National Academy of Sciences, USA, 105, 12938-12943.
Budd, M. (2002). *The aesthetic of nature*. Oxford: Oxford University Press.

Collias, N. E., and Collias, E. C. (1984). *Nest building and bird behavior*. Princeton: Princeton University Press.

Dutton, D. (2009). *The art instinct: Beauty, pleasure and human evolution*. New York: Bloomsbury Press.

Eibl-Eibesfeldt, I. (1988). The biological basis of aesthetics. In I. Rentschler, B. Herzberger, and D. Eppstein (Eds.), *Beauty and the brain: Biological aspects of aesthetics* (pp. 29-68). Basel, Germany: Birkhaeuser Verlag.

Endler, J. A. (2012). Bowerbirds, art and aesthetics: Are bowerbirds artists and do they have an aesthetic sense? *Science, 335*, 335-338.

Fisher, J. A. (1998). What the hills are alive with: In defense of the sounds of nature. The *Journal of aesthetics and art criticism, 56*, 167-179.

Frith, C. B., Frith, D. W., and Barnes, E. (2004). *The bowerbirds: Ptilonorhychidae*. Oxford and New York: Oxford University Press.

Goodfellow, P. (2011). *Avian architecture: How birds design, engineer and build*. Princeton and Oxford: Princeton University Press.

Gwinner, E. (1964). Untersuchungen ueber das Ausdrucks- und Sozialverhalten des Kolkraben (*Corvus corax*). *Zeitschrift fur Tierpsychologie, 21*, 657-748.

Haskell, M. (2000). *Bird nests and construction behaviour*. Cambridge: Cambridge University Press.

Heinrich, B. (1976). Foraging specializations of individual bumblebees. *Ecological Monographs, 46*, 105-128.

Heinrich, B. (1979a). *Bumblebee economics*. Cambridge, MA: Harvard University Press.

Heinrich, B. (1979b). “Majoring” and “minoring” by foraging bumblebees, *Bombus vagans*: An experimental analysis. *Ecology, 60*, 245-255.

Heinrich, B. (1995a). An experimental investigation of insight in the Common raven. *The Auk, 112*, 984-1003.

Heinrich, B. (1995b). Neophilia and exploration in juvenile common ravens, (*Corvus corax*). *Animal Behaviour, 50*, 695-704.

Heinrich, B. (2010). *The nesting season: Cuckoos, cuckolds and the invention of monogamy*. Cambridge, MA: Harvard University Press.

Heinrich, B. (2013). Why does a hawk build with green nesting material? *Northeastern Naturalist, 20*, 209-218.

Heinrich, B., and S. L., Collins. (1983). Caterpillar leaf damage and the game of hide-and-seek with birds. *Ecology, 64*, 592-602.

Heinrich, B., Marzluft, J., and Adams, W. (1996). Fear and food recognition in naïve common ravens. *The Auk, 112*, 499-503.

Heinrich, B., Mudge, P., and Deringis, P. (1977). A laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. *Behavioral Ecology and Sociobiology, 2*, 247-266

Kaplan, S. (1992). Environmental preferences in a knowledge-seeking, knowledge-using organism. In J. H. Barkow, L. Cosmides, and J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 581-591). New York: Oxford University Press.
Kessel, E. L. (1955). The mating habits of balloon flies (Diptera: Empididae). Systematic Zoology, 4, 97-104.

Kuspit, D. (2004). The end of art. Cambridge, MA: Cambridge University Press.

Langridge, K. (2006). Symmetrical crypsis and asymmetric signaling in the cuttlefish, Sepia officinalis. Proceedings of the Royal Society B, 273, 959-967.

Lenain, T. (1997). Monkey painting. London: Reaktion Books.

Lestel, D. (2011). Non-human artistic practices: A challenge to the social science of the future. Social Science Information, 50, 505-512.

Lewis-William, D. (2004). The mind in the cave: Consciousness and the origin of art. London: Thames and Hudson.

Ligon, J. D., Thornhill, R., Zuk, M., and Johnson, K. (1990). Male-male competition and male ornamentation in red jungle fowl. Animal Behavior, 40, 367-373.

Little, A. C., and Jones, B. C. (2003). Evidence against perceptual bias views for symmetry preferences in human face. Proceedings of the Royal Society London B, 270, 1759-1763.

Louv, R. (2008). Last child in the woods. Chapel Hill, NC: Algonquin Books.

Lyons, D. M., Titus, K., and Mosher, J. A. (1986). Sprig delivery by Broad-winged hawks. Wilson Bulletin, 98, 469-471.

Lyons, E. (1983). Demographic correlates of landscape preferences. Environment and Behavior, 15, 487-511.

Menzel, R., and Erber, J. (1972). The influence of quantity of reward on the learning performance in honeybees. Behaviour, 41, 27-42.

Morris, D. (1962). The biology of art: A study of the picture-making behavior of the great apes and its relationship to human art. London: Cox and Wyman, Ltd.

Orians, G. H., and Heerwagen, J. H. (1992). Evolved responses to landscapes. In J. H. Barkow, L. Cosmides, and J. Tooby, (Eds.), The adapted mind. New York: Oxford University Press.

Pijanowski, B. C., Villaneuva-Rivera, L. J., Dumyahn, S. L., Farina, A., Krause, B. L., Napoletano, B. N., . . . Pieretti, N. (2011). Soundscape ecology: The science of sound in the landscape. BioScience, 61, 203-216.

Real, R. G., Ianazzi, R., Kamil, A. C., and B., Heinrich. (1984). Discrimination and generalization of leaf damage by blue jays (Cyanocitta cristata). Animal Learning and Behavior, 12, 202-208.

Rensch, B. (1957). Aesthetische Faktoren bei Farb- und Formbevorzugungen von Affen. Zeitschrift fur Tierpsychologie, 14, 71-99.

Rodriguez, I., Gumbert, A., Hempel de Ibarro, N., Kunze, J., and Giurfa, M. (2004). Naturwissenschaften, 9, 374-377.

Samuels, C. A., Butterworth, B., Roberts, T., Grauper, L., and Hole, G. (1994). Facial aesthetics: Babies prefer attractiveness to symmetry. Perception, 23, 823-831.

Scharfstein, B.-A. (2009). Art without borders: A philosophical exploration of art and humanity. Chicago: University of Chicago Press.

Thornhill, R. (2003). Darwinian aesthetics informs traditional aesthetics. In K. Grammer and D. Voland (Eds), Evolutionary aesthetics (pp. 9-38). Berlin, Germany: Springer-Verlag.

Thornhill, R., and Moller, A. P. (1998). The relative importance of size and symmetry in
sexual selection. *Behavioral Ecology*, 9, 546-551.
Tolstoy, L. (1996, first published in 1896). What is art? *Philosophical Review*, 79, 334-367.
Verpooten, J., and Nelissen, M. (2012). Sensory exploitation: Underestimated in the evolution of art as once in sexual selection? In K. S. Plaisance and T. A. C. Reydon (Eds.), *Philosophy of Behavioral Biology. Boston Studies in the Philosophy of Science*, 282, 189-216.
von Frisch, K. (1954). *The dancing bees: An account of the life and senses of the honey bee*. London: Methuen.
Watanabe, S. (2010). Pigeons can discriminate “good” and “bad” paintings by children. *Animal Cognition, 13*, 75-85.
Watanabe, S. (2011). Discrimination of painting style and quality: Pigeons use different strategies for different tasks. *Animal Cognition, 14*, 797-808.
Wilson, E. O. (1984). *Biophilia*. Cambridge, MA. Harvard University Press.
Wilson, E. O. (2004). *The future of life*. New York: Random House
Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology, 53*, 205-214.