APA Handbooks in Psychology

APA Handbook of Comparative Psychology

VOLUME 1

Basic Concepts, Methods, Neural Substrate, and Behavior

Josep Call, *Editor-in-Chief*
Gordon M. Burghardt, Irene M. Pepperberg, Charles T. Snowdon, and Thomas Zentall, *Associate Editors*

American Psychological Association • Washington, DC

CHAPTER 37

COURTSHIP AND MATE CHOICE

Michael J. Ryan and Lyndon A. Jordan

The deceptively simple act of choosing among mates involves a range of behaviors and tasks, each of which has implications across an animal's psychology and biology. We review the proximate mechanisms underlying courtship and mate choice, including neurobiological and psychological factors, as well as our current understanding of the selection forces that influence mate choice evolution. A primary theme of our review is that our understanding of mechanisms and evolution need to be integrated to fully understand how and why animals court and choose mates the way they do.

COURTSHIP AND CHOICE

Courtship is a series of behaviors used by one individual, the courter, to elicit a sexual response, including mate choice, from another individual, the chooser. Often these roles are sex-specific, but there are numerous cases of mutual courtship and choice, our own species being one of the best examples (Miller, 1998). Courtship is modulated by, and feeds back on, fundamental physiological mechanisms that prepare the courter and the chooser for reproduction. Courtship also informs, seduces, and persuades the chooser to mate. Mate choice is the decision made by one individual, the chooser, about whether and with whom to mate (Kirkpatrick, Rand, & Ryan, 2006). The chooser decides who is attractive, and the chooser's percepts of attractiveness are influenced by its hormonal state, early and recent experience, and biases in its neural and cognitive systems. To understand why there is courtship, we first need to understand why there are two sexes (Ryan, 1997).

Although males and females often differ in numerous external characteristics (Darwin, 1871), the diagnostic character of sex—as opposed to gender which involves culturally acquired characteristics—is gamete size. Males have many small gametes and females have few large ones. This difference in gamete size has cascading effects on numerous aspects of an animal's reproductive behavior, including courtship and mate choice.

In a classic study on male and female reproductive strategies, Bateman (1948) showed that in fruit flies (*Drosophila*) the number of offspring sired by males increases dramatically with the number of females they mate, but beyond a certain threshold, the number of matings by females has a much smaller influence on female reproductive success. Although there are some species in which the number of matings can influence female reproductive success (reviewed by Arnqvist & Nilsson, 2000), the general pattern is that the number of matings has a greater influence on the reproductive success of males than females.

Trivers (1972) built on Bateman's (1948) principle and argued that differences in gamete size result in differences in parental investment. Females invest considerably more time and energy in eggs than males do in sperm which, in turn, limits reproductive opportunities for females. Trivers predicted that males should evolve strategies to maximize their number of mates, whereas females should evolve to maximize the quality of their mates. These different

http://dx.doi.org/10.1037/0000011-037
APA Handbook of Comparative Psychology: Vol. 1. Basic Concepts, Methods, Neural Substrate, and Behavior, J. Call (Editor-in-Chief)

strategies give rise to a fundamental conflict between the sexes over the optimal number of matings, which drives the evolution of sexual dimorphism under sexual selection (Arnqvist & Rowe, 2005).

Emlen and Oring (1977) extended this line reasoning to ecological conditions. Because females invest more in gametes, the ratio of females to males available for mating at any one time will be skewed toward males. It is this *operational sex ratio* that determines the degree to which females become the limiting sex and males become the limited sex; by this, we mean that the number of reproductively active females limits the reproductive opportunities for males and not vice versa. The operational sex ratio will become more skewed, fewer females to more males, when female reproductive activity in the population is asynchronous across a breeding season because only a small fraction of females in the population are available to mate at any one time, whereas males are continually in the mating pool. This, in turn, makes it more likely that fewer males can mate more females, leading to a greater reproductive skew. Emlen and Oring also predicted how ecological conditions would influence the manner and the intensity in which males compete for access to females, which they termed the *environmental potential for polygamy*. When resources required by one sex are clumped in space and time, for example, it is more likely for fewer males to control a majority of resources and thus have access to a majority of females compared to when resources are more evenly distributed.

A legion of studies has borne out the basic predictions of Bateman, Trivers, and Emlen and Oring (Andersson, 1994; Andersson & Simmons, 2006), and even the exceptions tend to prove the rule. For example, in fishes of the family *Sygnathidae* (seahorses, pipefish, and sea dragons), males become "pregnant" as the female deposits fertilized eggs inside the male's brood pouch where the eggs develop, preventing males from mating again quickly, and thus males become the limiting sex. In these sexual role-reversed species, females court males and males choose mates, and the number of matings has a greater influence on female reproductive success than on male reproductive success (Jones, Rosenqvist, Berglund, Arnold, & Avise, 2000).

In species with biparental or paternal care the asymmetry in investment is less and mutual mate choice can result. Mutual mate choice occurs in our own species, but is well investigated in a variety of animals. In zebra finches (*Taeniopygia guttata*), males and females contribute to parental care, and mutual mate choice is the rule (e.g., ten Cate, Verzijden, & Etman, 2006). In sticklebacks (*Gasterosteus aculeatus*), a species with paternal care, males are choosy and prefer to mate with females with larger eggs (Kraak & Bakker, 1998). Even in species with little parental care, opportunity costs and other risks of mating may drive males to carefully select with whom they will attempt to mate. In the golden orb weaving spider (*Nephila plumipes*), for example, males run an extremely high risk of being eaten during mating, and will carefully select among available females to maximize the reproductive benefits of their mate choices (Jordan et al., 2014).

The existence of two sexes is defined by gamete size. The difference in gamete size and many of the other differences between the sexes arises from a conflict of interest. This is one of the fundamental outcomes of the evolution of reproduction and is the foundation for all research into courtship and mate choice.

Physiological Bases and Function of Courtship

Courtship provides a platform for choosers to assess mates but may have a more general function. Courtship also plays a vital role in stimulating reproduction and synchronizing the physiological states of the sexes, a role that is often ignored in studies of behavioral ecology.

Animals do not breed at random. Most have breeding seasons during which males and females are in physiological reproductive condition and environmental conditions are favorable for mating, reproduction, and development of offspring. Hormones play an important role in synchronizing the seasonality of breeding. In many species of temperate zone mammals, for example, short or long day length triggers an increase in androgen levels that prepare males for either the spring or autumn breeding season (Bronson, 1989). One of the most important roles of courtship is to synchronize breeding at a much finer time scale.

Lehrman's (1996) classic study of courtship in ring doves combined with the continuing studies by Cheng (2008) offered the most detailed documentation of how this can be accomplished. Lehrman showed that courtship in ring doves consists of a series of interactions between the sexes that begins with males "bow-cooing" to females, females eventually join in a vocal duet with the male, and then the male and female copulate, build a nest, incubate the eggs, and feed the young. Figure 37.1 illustrates the complex interaction between behaviors and hormones within and between the sexes.

Cheng's (2008) subsequent work revealed further intricacies in this system. The male's bow-coo does not directly trigger the rise in the female's estrogen. It is her vocal response to the male, or more specifically her hearing her own vocal response, which causes a surge in gonadotropin-releasing hormone which leads to production of follicle-stimulating and lutenizing hormones. These latter two hormones then bring about an increase

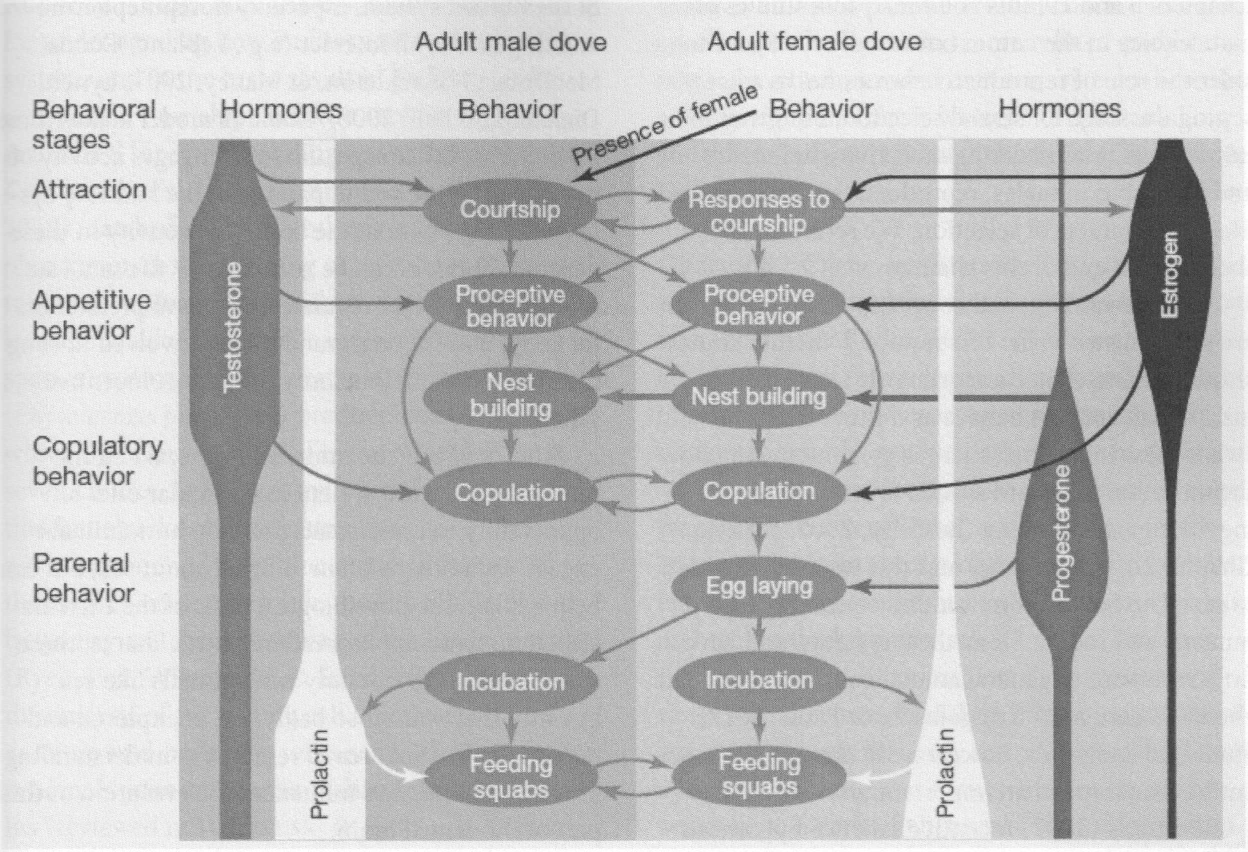

FIGURE 37.1. A male ringdove initiates courtship by producing a "bow coo" display as he struts toward the female and bows to her. This vocal signal is stimulated by the presence of a female. Initially the female will avoid the male until he locates himself at a potential nest site and produces a softer "nest coo." The female will then approach the male. The male now abandons the nest and coos, struts, and chases after the female as he produces a bow coo. Once again, the female flees. This ritual repeats itself, and in a day or two the male does not chase the female but instead allows her to participate in a nest-cooing duet. The duet lasts for a day or two, during which time the male gathers nesting material while the female continues to coo on her own. Copulation takes place sometime after the female approaches the male and before she produces solo coos. Three to five days later, she produces a clutch of eggs. Thereafter, the bonded pair cares for the eggs and later the nestlings. At each stage, the transition from one behavior to the next depends on a behavioral response from the opposite sex. From *Biological Psychology* (p. 417), by M. R. Rosenzweig, A. L. Leiman, and S. M. Breedlove, 1996, Sunderland, MA: Sinauer. Copyright 1996 by Sinauer Associates. Reprinted with permission.

in estrogen. Amazingly, this cascade is not initiated unless the female knows that the male is directing his courtship at her, and she ascertains this by observing the direction of his eyes (see Volume 2, Chapter 32, this handbook).

Sex steroids motivate male and female sexual behavior in a variety of systems. Recently, Schlinger et al. (2013) showed how the unusual acoustic and visual displays of the red-capped manakin (*Ceratopipra mentalis*) are modulated by sex steroids, and Wade (2012) showed how male courtship behavior and female receptivity in anolis lizards are also under the influence of steroid hormones (see Chapters 5 and 19, this volume). Most studies of mate choice in the context of sexual selection consider the role of reproductive hormones as merely setting the stage for sexual selection, but given their importance in modulating receptivity in females and courtship in males, reproductive hormones are likely also targets of selection. We return to this theme at the end of this chapter.

Sex is rewarding, and courtship and mate choice are mechanisms to get this reward. Whether courtship and mate choice are primarily learned or instinctual, animals behave as if they "like" and "want" sex. In general, there is great interest in how the mesolimbic reward system is involved in learning, liking, and wanting (Berridge, 2007; see also Chapter 23, this volume) and this interest extends to sex. The bulk of these studies concentrate on humans and rodent biomedical systems, and have little relevance to general animal courtship and mate choice (Georgiadis, Kringelbach, & Pfaus, 2012). Studies of songbirds, however, are changing that scientific landscape in an important way.

Berridge's (2007) incentive salience hypothesis suggests that dopamine's role in the mesolimbic reward system is not in generating hedonic pleasure (i.e., liking) but in modulating incentive salience (i.e., wanting). Maney (2013) adapted this model to investigate how norepinephrine and dopamine interact with songbird courtship vocalizations. An important point Maney made at the outset is that learning is not necessary for liking and wanting. For example, Woolley (2012) reviewed the importance of early experience in acquisition of and preferences for song in song birds (see Chapter 26, this volume), but also notes that many songbirds have innate perceptual biases to conspecific signals, a phenomenon that is widespread throughout the animal kingdom and across sensory modalities (Ryan & Cummings, 2013; see also Volume 2, Chapters 2, 3, and 4, this handbook).

Maney (2013) suggested that female attraction to conspecific courtship signals is evidence that they find courtship signals rewarding, that they like it. The reward system increases the motivation to respond to the courtship, it makes them want it. There is accumulating evidence that courtship signals, steroid hormones, and catecholoamines of the reward system, especially norepinepherine and dopamine, all interact (e.g., LeBlanc, Goode, MacDougall-Shackleton, & Maney, 2007; Lynch, Diekamp, & Ball, 2008). Maney's model makes three predictions: (a) conspecific song engages activity of norepinepherine and dopamine in the auditory system and elsewhere in the brain, (b) activity in these neuromodulators can be regulated by the same steroid hormones that regulate behavioral preferences for song, and (c) neuromodulators involved in song discrimination and memory may affect incentive salience.

Studies of catecholamines in general and the mesolimbic reward system in particular offer an opportunity to understand not only how animals engage each other's brain to bring about sex, but can help explain the physiological basis of the extreme sexual motivation observed in nature; that is, these studies can show not only why animals like sex but why they want it so badly. An unexplored and potentially fruitful area of research is understanding how sexual selection influences the evolution of this part of the sexual brain.

Sensory Modalities of Mate Recognition

Successful reproduction requires an individual and its partner not only be in a proper physiological state but also recognize who is an appropriate mate. Of paramount importance is mating with a conspecific rather than a heterospecific, as matings between heterospecifics usually do not result in the production of viable offspring. There are exceptions in which hybridization occurs and hybrids are more fit than parental species, and these successful hybridizations provide an opportunity for major and rapid evolution (P. R. Grant & Grant, 1992). These exceptions are more numerous than once thought (e.g., Culumber et al., 2011), but they are not the rule. Most males have species-specific courtship signals that are reliable indicators of species status. All of the major sensory modalities have been recruited for mate recognition and a number of studies have shown how sensory systems bias the response of females to conspecifics in favor of heterospecifics. We review some examples for each of the major modalities as follows.

Auditory. Frogs offer the best known system for understanding how auditory biases in sensory systems and in the brain result in preferences for conspecific courtship, and also serve as a general model for understanding this interaction. Capranica's (Frishkopf, Capranica, & Goldstein, 1968) matched-filters hypothesis is based on the observation that the tuning of the two auditory inner ear organs, the amphibian papilla and basilar papilla match the dominant frequencies in the species' mating call. For example, túngara frogs (*Physalaemus pustulosus*) produce a call with a whine that can be followed by no chucks or up to seven chucks. A whine is sufficient for mate attraction but chucks enhance attractiveness. The dominant frequency of the whine matches the tuning of the amphibian papilla while the chuck's dominant frequency matches the tuning of the basilar papilla (Ryan, Fox, Wilczynski, & Rand, 1990). Much of the analysis of the mating call takes place in the auditory mid-brain, the torus semi circularis, which is homologous to the mammalian inferior colliculus (reviewed in Wilczynski & Ryan, 2010). Here, there are neurons that are most responsive to combinations of spectral and temporal characteristics of conspecific calls and relatively unresponsive to sounds of less biological salience, such as environmental noise and heterospecific calls. Hoke and colleagues (2004) showed that immediate early gene responses (a proxy for neural excitation) in the torus of túngara frogs were greatest in response to conspecific calls. Lynch and Wilczynski (2008) also showed a critical link between the auditory and reproductive hormone systems as there is hormonal modulation of auditory responses by estrogen in the torus that matched the female's behavioral response. In general, the auditory midbrain appears to play an important role in controlling behavioral responses to acoustic social signals by acting as a regulatory gateway between the stimulus analysis of the brainstem and the behavioral and physiological control centers of the forebrain.

Frogs, of course, are not the only system in which the auditory basis of species recognition has been worked out in detail. Crickets (*Gryllidae*), in particular, share the general theme previously reviewed in frogs in which sensory end organs are tuned to stimulus parameters that characterize the species-specific signal and more refined analysis takes place in the central nervous system where the sensory input interfaces with the decision making and motor output regions of the brain (Gerhardt & Huber, 2002).

Olfactory. Chemosensory mate recognition is widespread in numerous vertebrate and invertebrate taxa (Smadja & Butlin, 2009). As frogs and crickets are ideal system for understanding neural circuitry of receivers, chemosensory systems are ideal for understanding the genetic components of the signal.

One of the best examples of how olfactory mate recognition can result in conspecific mate preferences comes from studies of the European corn borers, the adzuki bean borer moth (*Ostrinia scapulalis*) and the burdock borer moth (*O. zealis*; Tabata & Ishikawa, 2005). In moths, females produce long range advertisement signals to attract males. The antennae contain olfactory receptors that bind with specific blends of pheromones and are especially sensitive to blends of chemicals. Neural excitation is passed from the antennae to the mushroom body where identification of the pheromone is determined. The pheromone of *O. scapulalis* is a mixture of two tetradecenyl acetates (E11 and Z11). There are three separate phenotypes of pheromone blends in this species, E (99% E), I (64% E), and Z (3% E), which are determined by one autosomal locus with two alleles. *O. zealis* has a third compound (Z9) and its pheromone is a blend of this compound with E11 and Z11 in a typical ratio of 65% Z9, 30% E11, and 5% Z11. The two species do not cross in the wild, because of lack of mate recognition, but laboratory hybrids lack Z9, suggesting a simple recessive chromosomal factor (or factors). These studies show how a single mutation can lead to the divergence of courtship signals which results in lack of genetic exchange between populations and thus initiates the origin of species.

Visual. In numerous species, male courtship involves display of a variety of colors, ornaments, and motor patterns such as courtship dances in birds and push up displays in lizards. The link between male visual displays and mating preferences is most firmly established in fishes, and these studies also show how the environment biases visual tuning, which in turn influences courtship signals and can also influence speciation (reviewed in Ryan & Cummings, 2013).

In fishes, photopigment sensitivity can evolve in response to ambient light which, as has been shown in surfperch (*Embiotocidae*; Cummings, 2007) and sticklebacks (*Gasterosteus aculeatus*; Boughman, 2001), can then have an incidental influence on mate choice. These studies highlight the fact that the sensory organs and the brain function in numerous domains, mate choice being only one of them, and that evolution in one domain (e.g., visual scene detection) can influence how functions operate in other domains (e.g., mate choice).

An excellent example of these types of interactions occurs in cichlid fishes of the African Great Lakes. Seehausen and colleagues (2008) showed that in Lake Victoria the cichlid *Pundamilia* can range from near the surface to 8 m in depth and from red to blue in color. In general, light attenuates more on the blue (short wavelength) and red (long wavelength) ends of the spectrum with increasing water depth, and attenuation of long wavelengths is enhanced by more particulate matter in the water. These fishes tend to lose their red and blue coloration when inhabiting sites that are deeper and more polluted. Accompanying this change in color is a change in the sequence variation of the red-sensitive photopigment that yields two major allelic variants that differ by about 15 nm in peak sensitivity. The blue-shifted photopigment is more common in shallow water dominated by males with blue nuptial coloration, whereas the red-shifted photopigment is more common in deeper water in which red males dominate. Populations that range over a greater depth have both alleles. The researchers have shown that color-based mating preferences covary with photopigment sensitivity. In one shallow population in which blue males and blue-shifted photopigment alleles dominate, most females exhibit mate choice preferences for the blue phenotype, while at another site with a polymorphism in color and photopigment sensitivity, there is also a polymorphism in female preference. These studies of fishes are only one example of many that illustrate how selection in other domains can incidentally drive the evolution of mate choice and the courtship traits that are deemed attractive (Ryan & Cummings, 2013).

Multimodal. Most animals live in a world that demands the attention of multiple sensory modalities, but only recently have researchers began to address how animals assess multimodal signals in courtship (Higham & Hebets, 2013). Excellent analyses of multimodal courtship have been conducted in fruit flies (*Drosphila*; Billeter & Levine, 2013), spiders (*Schizocosa*; Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013), frogs (*Anura*; Preininger et al., 2013), and birds (*Molothrus ater*; O'Loghlen & Rothstein, 2010).

As discussed previously, the function and mechanisms of acoustic mate recognition in frogs is well understood, but túngara frogs, for example, also recruit at least two other sensory modalities in mate assessment. In both cases, these cues did not evolve for communicative function but, instead, are incidentally associated with calling. In humans, we move our lips as we talk to expel air and to modify the acoustic waveform of the voiced speech, but the evolved function of human lip movement is not to transmit information. Lips movements, however, have been recruited by receivers to extract additional information (McGurk & MacDonald, 1976). A similar phenomenon occurs in other animals. For example, when frogs call, the vocal sac inflates and deflates and in several species this visual cue influences the response of receivers to the mating display (Starnberger, Preininger, & Hödl, 2014). The interactions between acoustic and visual cues can be surprisingly nonlinear. Túngara frog females find a whine–chuck mating call more attractive when it is paired with the synchronously inflating and deflating vocal sac, but if the inflation cycle is not synchronous with the call this visual cue does not add attractiveness (Taylor & Ryan, 2013; see Figure 37.2). A similar effect takes place within the call itself; a chuck following a whine makes the call more attractive but if the chuck is displaced in time it no longer enhances the whine. Surprisingly, if the vocal sac inflation and the chuck are displaced so they are in sequence, then salience is restored to the visual cue and the chuck, probably by instilling some type of perceptual continuity (Taylor & Ryan, 2013). The fact that females find this unnatural stimulus attractive leads us to question some of the basic models involving internal templates for signal recognition (Marler, 1997), and highlights how hidden preferences as yet unstimulated by existing signals can drive the evolution of courtship displays in unpredictable directions. A recent study shows that the inflation and deflation of the vocal sac also produces ripples on the water's surface which are then also attended to by the receiver (Halfwerk, Jones, Taylor, Ryan, & Page, 2014) suggesting that there might be numerous unexplored modalities being used in mate assessment.

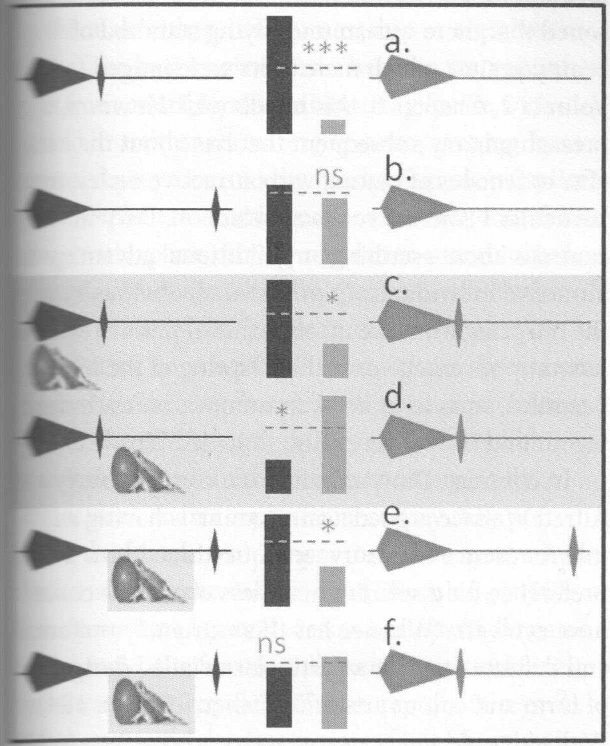

FIGURE 37.2. Female túngara frogs prefer (a) a whine-chuck to a whine, (b) but when the chuck is displaced from the whine it is no longer more attractive. (c) Females prefer a whine-chuck with an inflating vocal sac compared to the same call with no visual cue, (d) but when the vocal sac is displaced from the call it no longer makes it more attractive. Surprisingly, when we combine the two signals with the displaced chuck and the displaced vocal sac inflation (b & d), then (e) the positive effects of both cues are "rescued" and (f) this unnatural stimulus is as attractive as a normal whine-chuck. From "Interactions of Multisensory Components Perceptually Rescue Túngara Frog Mating Signals," by R. Taylor and M. Ryan, 2013, *Science*, *341*, pp. 273–274. Copyright 2013 by the American Association for the Advancement of Science. Adapted with permission.

Learning mates. Although nature–nurture is an outdated dichotomy (Robinson, 2004; see also Chapter 18, this volume), the mating systems previously discussed are thought to be influenced by a large genetic component with smaller environment and gene-by-environment effect. A stark contrast to these systems are ones in which early exposure to the courtship of conspecifics influences later mate preferences. Perhaps the most extreme case occurred when graylag geese (*Anser anser*) imprinted on Konrad Lorenz and followed him around his institute as if he were their mother (Lorenz & Taylor, 1977).

The best understood system is song learning in birds. Marler and his colleagues (Marler, 1976; see also Chapters 3 and 26, this volume) used Kaspar Hauser experiments in which white crowned sparrows were deprived of hearing conspecific song during specific periods of time. These studies revealed a fairly restricted "sensitive" period during which song was acquired even though it was not until weeks later that the birds actually sang. Without song exposure during the sensitive period, males did not later produce species-typical song. Song birds are a very large group with about 4,000 species, so not surprisingly there is variation among species in the timing of song learning, if they learn single songs or song repertoires, and to what degree songs can be elaborated later in life (Beecher & Brenowitz, 2005; Brenowitz & Beecher, 2005).

Most songbird learning studies have concentrated on the male. Although it is tacitly assumed that females learn the song they later prefer, there is far less evidence for this, the best coming from studies of zebra finches (*Taeniopygia guttata*). In one example, Riebel and colleagues (2009) showed that female zebra finches exhibited a preference for tutor song over nontutor song, but in the absence of tutor song they were attracted to nontutor song.

The influence of early experience on later mating preferences is more widespread than once appreciated, and is certainly not restricted to birds. Hebets (2003) showed that mate preferences of female wolf spiders (*Schizocosa*) were influenced by early exposure to adult males; females preferred to mate with more familiar phenotypes. In an extremely odd case, Verzijden and ten Cate (2007) studied the effect of experience on the young of mouth brooding cichlids (*Pundamilia*). The researchers did cross-fostering experiments in which offspring were mouth-brooded by a female of a different species. When the young females later reached maturity, they showed mate preferences for males of the foreign species which brooded them over males of their own species.

Evolution of Mate Choice

Darwin's theory of sexual selection is driven by the dual processes of intersexual mate choice and intrasexual competition for mates. Competition for access to mates has led to the stunning proliferation of weapons and tactics throughout the natural world, and the process of mate choice has generated some of the most spectacular and memorable display traits in animals. Although the benefit of large tusks, antlers, and claws in competition for mates is obvious, the reasons that a female should prefer a complex song repertoire, a particular pheromonal bouquet, or bright gaudy colors are less obvious. Many of the traits that are used in mate choice carry an obvious survival cost to the bearer, reducing their ability to escape predators or increasing the opportunity cost of foraging, making their evolution an even greater puzzle. In this section, we explore how the costs and benefits of choosing among mates have shaped the evolution of mate choice across taxa.

Darwin's sexual aesthetics and Wallace's skepticism. An early justification for mate choice was that animals chose the most inherently beautiful mates. Charles Darwin (1871) described females choosing among males on the basis of sexual aesthetics or particular standards of beauty, stating "I have attributed [the males'] beauty to the females for many generations having chosen and paired with the more attractive males" (p. 318). He reasoned that the aesthetic capacity of females developed over time to appreciate certain ornaments in males, and these preferences were then used to choose among potential mates. Although careful to state that the standards of beauty need not be the same for humans and animals, Darwin nevertheless reasoned that there was an underlying standard of beauty against which male traits were judged (see Volume 2, Chapter 6, this handbook). However, presaging many subsequent theories about the benefits to females of mating with attractive males, in particular Fisherian runaway selection, Darwin was cautious about ascribing any additional advantage to attractive individuals: "Nor is it at all obvious how the offspring from the more beautiful pairs . . . would have any advantage over the offspring of the less beautiful, so as to increase in number, unless indeed vigour and beauty generally coincided" (p. 327).

In contrast, Darwin's scientific contemporary Alfred Wallace argued against animals having an inherent sense of beauty, and questioned how a preference for a seemingly useless ornament could have evolved: "Whence has this extremely uniform and definite taste for a particular detailed design of form and colour arisen?" (Fisher, 1915, p. 184). Wallace could not see an adaptive advantage associated with mate choices on the basis of an arbitrary sense of beauty. In fact, his particular spiritual leanings (which later manifested in an extreme interest in the occult) led him to reject outright Darwin's claims that an aesthetic sense could occur in animals, it being a strictly human trait associated with the "spiritual nature" of man and developed independently of his "animal nature."

In the time since this initial disagreement over how and why mate choice systems have evolved, a vast body of theory and empirical evidence have been generated, and our understanding of mate choice has greatly increased. The benefits of mate choice fall into two major categories on the basis of the timing and recipient of the benefit. The first, and relatively uncontroversial form is that of a chooser gaining direct benefits of choice (e.g., increase in the number of offspring produced). The second form, subject to much greater debate and inherently harder to measure, occurs when the chooser does not benefit directly, but when benefits are accrued indirectly through traits of offspring.

Direct selection. A female's mate choice can increase her reproductive output when her partner provides some material benefit. Typically, these benefits come in the form of material resource provided by the male either during courtship or copulation. One of the best known direct benefits are nuptial gifts from courting males. Nuptial gifts are widespread in arthropod mating systems, ranging from captured prey items to the production of specialized *spermatophores*—nutritional compounds transferred along with sperm during copulation—and include examples from some spider species in which the male is eaten by the female immediately after or even during copulation. The nutritional direct benefit to the choosing female is obvious, and in some species the effect of gift quality on female choice is well described. In the predatory scorpionfly (*Bittacidae*), males capture insect prey they present to the female with whom they then mate while the female eats the nuptial gift (Thornhill, 1976). If the prey item is small, or has been partially eaten by the male, the female will exercise mate choice by terminating copulation more rapidly (Gwynne, 1984), reducing the proportion of her eggs that are fertilized by that male. The evolution of mating systems with nuptial gifts has taken a peculiar detour in some groups like the dance flies (*Empididae*), where genuine gifts have been replaced with "tokens"; arbitrary objects of no direct value to females. Some species in this family present actual prey items (including members of their own species) as gifts to females, and may do so by wrapping them in silk before presentation (e.g., *Hilara* spp.). Yet in other species in the family, the silken package contains inedible insect parts or nothing at all, hardly constituting an actual gift and providing the choosing female with no direct benefit. Although there are very important mechanisms that can generate preferences for arbitrary traits, which we discuss in the next section, the presentation of worthless gifts is thought only to evolve from systems in which genuine gifts were initially being given (Lebas & Hockham, 2005).

A more taxonomically widespread direct benefit of choice occurs when females base their mate choices on an ecologically relevant resource provided by the male. In pied flycatchers (*Ficedula hypoleuca*), age, size, plumage color, and song repertoires of males are of little influence in female choice, rather the single most important criterion for female choice among males is the quality of their territories (Alatalo, Lundberg, & Glynn, 1986). Similarly, in the cichlid fish (*Neolamprologus multifasciatus*) females preferentially join males who have added more empty snail shells to their nests—shells in which the female lays her eggs and uses to shelter her fry. Males must be careful however, as the risk of territory take over by larger predatory fish increases as he continues to add shells to his nest (Jordan, Maguire, Hofmann, & Kohda, in press). The benefit of choice need not be material however, and in many species, females select among males on the basis of condition-dependent traits, those that vary with respect to a male's health, vigor, or ability to find food. If females choose males in good physical condition, assessed on the basis of traits including plumage coloration, courtship endurance, and size, they may benefit by having partners who can provide food to their offspring, provide longer or better parental care, or be better at detecting and avoiding predators. Moreover, a male in good condition is less likely to carry parasites or disease that may be transferred to the female during copulation or pairing, constituting a direct benefit of choosing healthy males through reduced risk of sexually transmitted infection.

Finally, females may express preferences for traits that normally indicate a direct benefit in an ecological domain, such as a feeding context, that is unrelated to reproduction. Sensory drive describes the process in which females prefer certain male traits because they are biased toward them by sensory pathways that evolved in other contexts. An example comes from the colorful Trinidadian guppy (*Poecilia reticulate*), in which the female preference for males with a greater area of orange is thought to be a consequence of females' visual sensitivity to the orange of berries that occasionally drop into the water and provide a nutritional benefit (Rodd, Hughes, Grether, & Baril, 2002).

Indirect selection. The choice among potential mates may not be due to benefits the chooser acquires directly, but through indirect selection operating on traits in the next generation. The basic argument underlying indirect selection is that female choice does not influence the number of offspring produced but the quality of those offspring. One major difficulty is that, compared to benefits accrued through direct processes, measuring the costs and benefits of indirect selection is empirically extremely difficult, and even simulating the progression of associations between alleles over multiple generations is challenging. Despite these difficulties, there are a number of well-developed models of indirect selection acting on mate choice.

Genetic compatibility. The least controversial method of indirect selection involves processes that have a demonstrable and easily measurable effect on offspring fitness. As previously noted, matings with heterospecifics usually do not yield viable offspring because of genetic incompatibilities. Both courtship and mate recognition systems have evolved under strong selection to minimize these costs.

Genetic compatibility can also vary among partners within a species, and evidence has been accumulating that female choice assesses this criterion. Inbreeding avoidance will commonly lead to female preferences for mating with nonkin, although the mechanisms used to identify kin are likely to be specific to particular groups (Grob, Knapp, Martin, & Anzenberger, 1998), and may be based on nongenetic mechanisms like imprinting on parental types to identify self. Another emerging form of indirect selection comes in female preference for males on the basis of major histocompatibility complex (MHC). In house mice, females choose among mates on the basis of olfactory MHC cues (Wedekind & Füri, 1997), preferring males that have dissimilar MHC types to their own (Penn & Potts, 1999), a process thought to increase protection against pathogens. Yet, the indirect benefits to the choosing individual are not always so easy to measure.

Fisherian runaway selection. In a letter to Asa Grey, Darwin wrote that "The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Darwin, 1887, p. 296). He was speaking about the difficulty in understanding how a trait that so obviously reduced the chance of survival of the bearer could have been retained by selection. Across species, we observe that females frequently base mate choice on arbitrary traits, and the geneticist R. A. Fisher (1915, 1958) argued that female choice for a trait that is under negative natural selection (e.g., by reducing survival) may still be adaptive. Fisher posited that when the male trait and the female preference for that trait have a genetic basis, choosy females will pair up more frequently with males possessing the exaggerated trait. Through this process, the preference and the trait will become genetically (statistically) coupled and will coevolve to even more extreme versions of preference and trait. This process, modeled mathematically by Lande (1981), is known as *Fisherian runaway selection* because the process will continue to enhance the male trait until the benefit in a reproductive context is opposed by natural selection pressure, or until the genetic variance in either female preference or male trait become depleted. A major prediction of this type of model is that the display trait in the male becomes genetically linked with the preference in the female, and there are some studies that demonstrate this link (Wilkinson & Reillo, 1994). However, the continued impact of this theory comes more from historical importance than overwhelming support for it (Kirkpatrick & Ryan, 1991).

Indicator, handicap, and good genes models. An alternative group of models characterizing how female mate preferences may generate indirect benefits are based on "good genes" arguments, which are themselves based on the handicap principle. The argument centers around the fact that secondary sexual characters are costly, and so only individuals in good condition are able to bear the costs of developing and bearing these traits. The honesty and reliability of the signal is maintained by the differential costs they have for high- and low-quality individuals, governed by their genetic constitution (Zahavi, 1975). A preference for exaggerated traits will therefore indirectly select for individuals of higher "genetic quality," as the extreme viability selection acting against these traits will prevent low-quality individuals from expressing the preferred character. A related model is the parasite hypothesis, proposed by Hamilton and Zuk (1982), where the display trait functions as an indicator of a male's genetic resistance to parasite infection. The logic is similar to Zahavi's (1975) handicap in that males who are heavily parasitized are unable to express the trait with the same vigor as males with a higher genetic resistance to parasites. Thus, females may obtain reliable information about genetically based parasite resistance by using male secondary sexual characters as a basis for their mate choice, and females that mate with vigorous males gain an evolutionary advantage by passing these good genes to their offspring. Although there are a handful of studies consistent with this mechanism of sexual selection (Andersson, 1994), these are relatively rare when weighed against the considerable research effort dedicated to detecting these effects. A literature review on the topic revealed that the average variance in offspring viability explained by expression of males secondary sexual characters ranges between 1-2% (Møller & Alatalo, 1999).

Genic capture. One of the continuing controversies in sexual selection is the paradox of the lek (Kirkpatrick & Ryan, 1991). If females are exerting strong preferences for males with good genes for survivorship, then genetic variation for survival traits should become depleted. What maintains this genetic variation, if indeed it is maintained? The genic capture (Rowe & Houle, 1996) model proposes that when females choose among secondary sexual traits they may also "capture" genetic variation at numerous other loci that influence condition and thus gain partners and subsequently offspring with a genetic predisposition for survivorship.

Direct versus indirect benefits. Although the aforementioned models show that indirect selection can work, they make simplifying assumptions about behavior and genetics, meaning they are unlikely to effectively predict the reality of natural processes. A model by Kirkpatrick and Barton (1997) predicts the strength of indirect selection in shaping female mate preferences. The authors suggested that the force of indirect selection on mating preferences is weak and that direct selection on preference genes may often be more important than indirect selection. Unfortunately, there is a dearth of empirical data that allows direct comparisons of indirect versus direct fitness benefits accrued through mate choice.

Deceptive Courtship

That mate choice can be adaptive, either through direct or indirect benefits of choice, is undisputed. However, there are also numerous examples in which the choice among mates is a consequence of sensory biases that have evolved or been developed in other ecological domains. In these cases, the question of whether the chooser (often female) benefits is secondary to whether the male benefits, because the "choice" is based on deceptive processes. When males use food lures as sexual ornaments, the behavior of the females is an outcome of a sensory or cognitive circuit processing a feeding response, rather than one actively discriminating among potential sexual partners. It is distinct from sensory drive, in which an existing bias in the sensory architecture causes females to prefer mates with certain traits, but does not confuse traits in those mates as being, for example, a food source.

When the Asian corn borer moth *Ostrinia furnacalis* (*Pyraloidea, Crambidae*) hears the ultrasonic calls made by bats, their natural predators, they immediately stop moving to reduce being detected. Males of this species exploit this behavioral response to increase their mating success, producing an ultrasonic courtship song of extremely low-intensity that causes the female to freeze and allows males easy access for mating (Nakano, Takanashi, Skals, Surlykke, & Ishikawa, 2010). This behavior is taken a step further in the water strider *Gerris gracilicornis*, where males will actively attract real predators as long as a female rejects his mating attempts (Han & Jablonski, 2010). This behavior is thought to intimidate females into accepting matings to avoid the increased risk of predation associated with the male's courtship.

Sensory traps involving prey-related cues are somewhat more common. In several animals, including goodeid fishes (*Goodeidae*) and swordtail characins males possess physical or behavioral traits that mimic some aspect of a prey item to which the female is sensitive. Water mites are highly sensitive to vibrations on the water surface emitted by potential prey items. In goodeid fishes, males possess a yellow band at the terminus of their tail, used as part of the courtship display, which mimics the yellow worms on which these fish feed (Garcia & Ramirez, 2005). This ruse only works so long as it does not become too common; once this trait becomes fixed in a population and all males possess the yellow band, females no longer respond to the signal as a food item, only as a sexual display. Another example comes from Kolm and colleagues (2012), who showed that male swordtail characins use a highly-modified operculum cover to act as a food lure for females. Remarkably, the lure mimics the specific prey items found in each local population to attract females, with whom the males then attempt to mate.

Exploitation of signals can even span biological kingdoms. The flowers of *Ophrys* orchids have specialized adaptations to attract male *Andrena* bees as pollinators, and do so by exploiting male sensory bias toward the cues of females. The flowers contain no nectar reward, but rather produce chemical mimics of female sex pheromones that stimulate pseudocopulation with the floral corolla and effect pollination (Schiestl et al., 1999). The males receive no apparent benefit from this transaction, being completely duped by the deceptive signal.

Psychological Biases in Mate Choice

Deceptive courtship is one extreme example how biases in the chooser that are active in one domain, such as foraging, can be exploited by the courter. There are also other biases in the animal's psychology that contribute to biases in mate choice even though these biases might have arisen in other domains.

Supernormal stimuli. A supernormal stimulus is an exaggerated version of a stimulus that elicits a stronger response compared to the normal stimulus. Lorenz and Tinbergen (1970) showed that nesting graylag geese will preferentially retrieve a large ball into its nest than its actual smaller egg. This might not seem adaptive, but given the bird's nesting habitat a good rule of thumb is to retrieve large objects in the vicinity of the nest. In mate choice these types of preferences for the more extreme are often referred as open-ended preferences.

A classic example of this type of mate choice comes from studies by Magnus (1958) of frittilary butterflies (*Argynnis*). In this system males choose females and their choice is based in part on the female's wingbeat display. The typical wingbeat is from 8–10 Hz. Magnus showed with a flapping robot that males prefer faster wingbeats up to 140 Hz, which is also the flicker fusion rate of the butterfly's eye. Thus as long as he can perceive a faster wingbeat he prefers it. Why did this type of preference evolve? One possibility is that females with faster wingbeats deliver a fitness advantage to the choosing male. Another reason is that the neural circuitry underlying mate choice is stimulated by a more vigorous stimulus and this favors females to beat their wings faster. The males apparently receive no direct fitness advantage although they may produce more attractive daughters through Fisherian runaway selection. Many of the preferences for exaggerated traits fall into this category.

Novel traits. There are other cases in which females prefer traits that deviate from the typical conspecific courtship, and these are preferences for traits that are not found in the conspecific courtship display. One of the first demonstrations of preferences for novelty was when Burley showed that mate choice in female zebra finch was biased by the color of leg bands on the males, all of whom normally have uniformly orange colored legs (Burley, 1985). More oddly, she showed that males fitted with feathered hats were more attractive to females (Burley, 1985). Similarly, Gould, Elliott, Masters, and Mukerji (1999) altered models of male guppies (*Poecilia reticulata*) in numerous ways to reveal otherwise hidden preferences in female mosquito fish (*Gambusia*), and Ryan, Bernal, and Rand (2010) showed dozens of sounds besides chucks also enhanced the attractiveness of the túngara frog's whine. We already have discussed how stringing together typically incoherent visual and acoustic stimuli in an unnatural sequence in túngara frogs results in not only a salient but an attractive courtship display.

Experiments demonstrating preferences for novel displays are important because they mine the female's preference landscape to uncover preference peaks that have not been matched by existing male traits. These studies show there is immense potential for courtship preference to quickly select for certain traits as soon as they arise in males, rather than what we assume would be a slower, less likely process of mutations in preferences having to occur coincident with male traits as they arise. Hidden preferences and their exploitation by male traits might be one of the reasons that sexual selection seems to lead to rapid trait evolution.

Peak shift and character displacement. The psychological phenomenon of peak shift displacement (see Volume 2, Chapter 15, this handbook) has some similarities to the ethological ones of supernormal stimuli (Staddon, 1975), which was first demonstrated by Hanson (1959). In a classical conditioning experiment with pigeons, positive reinforcement was paired with a short wavelength of light (550 nm) and negative reinforcement with longer wavelengths. When later tested with a variety of light stimuli the peak positive response of the pigeon was not to the stimulus associated with the positive reward but with an even shorter wavelength, one that was more different from the negatively-reinforced longer wavelength. The adaptive advantage of peak shit displacement might be a generalized response to maximize avoidance of a negative reward.

Enquist and Arak (1993) showed how peak shift displacement could result in the evolution of extravagant sexual traits. They trained an artificial neural network to give a positive response to a stimulus resembling a long-tailed bird and a negative response to one resembling a short-tailed bird. After training was complete they presented the artificial neural networks with illustrations of birds with varying tail lengths. The strongest response was to an illustration with a super-long tail. ten Cate and Rowe (2007) reviewed numerous studies demonstrating the importance of peak shift in the everyday life of animals (see also Lynn, Cnaani, & Papaj, 2005).

Traits involved in courtship are usually sexually dimorphic and these traits are often the best indicators of an individual's sex. The first adults to which young are exposed are often their parents, who can then become models for forming percepts of male and female (see Volume 2, Chapter 5, this handbook). In zebra finches, males have red beaks and females have orange beaks. The young imprint on the beak color of each sex and use this information to determine sex. Later in life, males prefer mates not with a beak color similar to their mother's but with one most dissimilar from their father's. This *beak shift displacement* could further the evolution of sexual dimorphism in beak color (ten Cate, Verzijden, & Etman, 2006). A similar phenomenon occurs in female mate preference for number of song notes of male partners; females prefer males who produce more notes than did their father (Verzijden & ten Cate, 2007). Beak shift displacement could produce a phenomenon in evolutionary biology known as *reproductive character displacement* (P. R. Grant, 1972). In these situations, sympatric species show divergence of mating signals in a direct manner that reduces mismatings with heterospecifics, and can explain a shift in preferences away from the songs of an invading species in Galapagos finches (*Geospiza*; B. R. Grant & Grant, 2010).

Weber's law. Mate choice involves comparisons and many of these comparisons are based on the magnitude of differences in sexual traits, and females often prefer more of a trait, such as larger size, higher amplitudes, and faster display rates. To understand mate choice, we should understand something of the rules used in making these comparisons (see Volume 2, Chapters 1 and 25, this handbook).

Humans often compare stimulus quantities using proportional rather than absolute differences, a phenomenon known as *Weber's law* (Stevens, 1975). A consequence of this rule of thumb is that as stimulus magnitude increases the difference between stimuli required for them to be perceived as different increases. We can more easily discriminate the differences in lengths of lines that are 1 cm versus 2 cm, for example, than between lines of 1000 cm and 1001 cm. In mate choice, Weber's law could provide a cognitive brake on the evolution of trait magnitude, as large traits evolved into even larger ones, greater changes in magnitude would be required for a new trait to be considered more attractive (Cohen, 1984).

Only one study has documented Weber's law in mate choice (Akre, Farris, Lea, Page, & Ryan, 2011). Female túngara frogs prefer whines with more chucks to whines with fewer chucks. The pattern of preference is best explained by the proportional difference rather than the absolute difference in chuck number: Females showed a much stronger preference for 2 versus 1 chuck compared to 6 versus 5 chucks. Frog-eating bats (*Trachops cirrhosus*), who are searching for a meal rather than a mate, follow the same Weber function in their attraction to túngara frog calls suggesting that in both cases this rule of thumb is a result of a general cognitive algorithm common in many domains of many vertebrates, rather than a specific adaptation for mate choice or foraging. Akre and Johnsen (2014) reviewed the potential for Weber's law to bias evolution in mate choice as well as other domains in which animals compare stimulus magnitude.

Irrational mate choice. Decisions are supposed to make sense, to be rational. They should be made in a manner that maximizes some utility (see Volume 2, Chapters 15 and 16, this handbook). In human economics this utility is often financial benefit, whereas in evolutionary economics the utility is assumed to be Darwinian fitness. Virtually all research on mate choice makes the assumption that potential mates can be ranked on a one-dimensional scale of some preference function (Jennions & Petrie, 1997). If there is a rational or strict preference (Kirkpatrick, Rand, & Ryan, 2006), then the assigned preference or utility score should not be influenced by context. As an extension, two defining criteria for rational choice are transitivity and regularity.

Transitivity is an arithmetic property which states that if A>B and B>C then A>C (see Chapter 32, this volume and Volume 2, Chapter 18, this handbook). Surprisingly little has been done to document transitivity in mate choice. Kirkpatrick et al. (2006) analyzed preferences of túngara frogs for a series of natural mating calls. On one hand, their analysis showed that the frogs' preferences did not match any of the models of strict preference, although on the other hand the data did not show intransitivity in mate choice. These preferences in this study were at the population level rather than repeated measures with individual females. It is possible that individuals are intransitive but when such responses are summed they appear transitive.

The other criterion for rational choice, *regularity*, is violated when the relative preference for A over B changes in the presence of C. The presence of a competitive decoy, as C is generally known, is known to produce irrational choice in humans and in animals making foraging decisions (Bateson & Healy, 2005). The few attempts to investigate violations of regularity in mate choice have not offered strong support for a competitive decoy effect (Royle, Lindström, & Metcalfe, 2008). The sparse investigation of rationality in the domain of mate choice suggests we might be lacking a complete understanding of some of the basic psychological rules of how animals go about choosing their mates.

Social milieu. Mate choice takes place in a social environment which itself can influence perceptions of mate quality. Mate choice copying is one the most obvious social effects.

It is well known in humans that our value judgments are subject to peer pressure. In humans and animals, perception of an individual's attractiveness can be influenced by the broader sexual marketplace. Best documented in guppies, Dugatkin (1992) showed that the normal preference for males with more orange can be reversed when a female observes a typically less attractive male being courted by a female. There are limits to how far a female will change her preference, and in guppies it is a 20% difference in the amount of orange (Dugatkin, 1996). Numerous studies by evolutionary psychologists using photographs of members of the opposite sex show similar results. A man with an escort receives a higher attractiveness score than when alone, and the amount of boost depends on the attractiveness of his escort (Waynforth, 2007).

Closing time. The social environment is not constant and Pennebaker and his colleagues (1979) conducted a study that echoed the question of the country western singer Mickey Gilley: "Don't the girls get prettier at closin' time?" Men and women in a bar were asked to rate the attractiveness of members of their own and the opposite sex early on in the evening and then later toward closing time. Attractiveness ratings of opposite sex patrons, but not of same sex patrons, were higher later in the evening. A more recent study of this phenomenon accounts for a "beer goggles" effect. Although blood alcohol content influenced attractiveness scores in the direction one would expect, there was still a closing time effect (Johnco, Wheeler, & Taylor, 2010).

The closing time phenomenon is not restricted to humans. In many animals if a female fails to find a mate during her fertile period her entire reproductive investment is wasted. Thus a female's threshold for accepting a mate should be lower as this "closing time" approached, and this is just what we see in túngara frogs, as females only come to the breeding site to choose a mate on the day they will drop their eggs. Lynch, Rand, Ryan, and Wilczynski (2005) showed that a female's permissiveness, in terms of the qualities of a call that she finds attractive, peaks as she reaches the time when she must drop her eggs. This peak of permissiveness correlates to a rise in estrogen levels (Lynch, Crews, Ryan, & Wilczynski, 2006).

In our own species much attention is given to a woman's biological clock, which stops ticking with the onset of menopause and the end of her reproductive age. Middle-age women with "ticking clocks" think more about sex, have more frequent and intense fantasies about it, and have sex more often (Easton, Confer, Goetz, & Buss, 2010). In other animals, reproductive senescence precedes or occurs with death, which can be predicted by age. Here too females behave in a manner that increases the probability of reproducing before that final closing time. In cockroaches (*Blattaria*), older females need less courtship before they decide to mate (Moore & Moore, 2001). Similarly, older female guppies (Kodric-Brown & Nicoletto, 2001) and house crickets (*Gryllus*; Gray, 1999) become less choosy about a mate as they get older. As with the social milieu, time is one more axis of variation that generates diversity in mate choice within, as well as among, individuals.

THE PHYSIOLOGY OF REPRODUCTIVE STATE AND THE EVOLUTION OF ACTIVE MATE CHOICE

This review of courtship and mate choice has covered issues in the proximate and ultimate domains, the mechanisms underlying these behaviors, and their adaptive significance. We end this review with a consideration of how proximate and ultimate domains interact and feed back on one another, and of how their interactions could influence their evolution (Ryan & Wilczynski, 2014).

As reviewed earlier, proximate studies have identified in great detail how courtship signals release a cascade of events that influence a female's readiness to mate. We have also reviewed how ultimate studies of sexual selection by mate choice document how variation in male courtship signals can result in adaptive female mate choice. Despite the fact that both phenomena involve mate assessment rarely do the twain ever meet. The lack of integration here is surprising given, as Adkins-Regan (2005) pointed out, "gonads produce gametes and hormones, with the same hormones regulating gametogenesis and mating behavior" (p. 3). Accordingly, we outline here the degrees to which mechanistic processes involved in regulating reproductive state and those regulating mating behaviors might influence one another. We refer to the interaction between these two reproductive domains as varying from being associated (sharing common mechanisms, stimulus control, and/or sensory-response transformations) to disassociated (no such common processes).

An individual's reproductive state and its mate choice or mate attraction behaviors are usually addressed as separate phenomena that occur at different time scales, recruit different mechanisms, and evolve under the influence of different selection forces. Critically, they are also addressed by different research programs (e.g., Figure 37.3A and B), but they might be inextricably linked (Figure 37.3C). As previously noted, for example, male bird songs and frog calls influence steroid hormones critical for female and male reproduction (Cheng, 2008;

Sweeney & Kelley, 2014; Wingfield, Hegner, Dufty, & Ball, 1990) and these same courtship signals also influence mate choice by females and sexual advertisement by males (Catchpole & Slater, 2003; Gerhardt & Huber, 2002).

We can consider the degree to which the domains of reproductive state and mating behavior are mechanistically associated or disassociated by examining the extent to which they rely on the same signals and neural processing systems (Ryan & Wilczynski, 2014). Sexual signals are perceived by an end organ of the sensory channel, such as the eye or the inner ear. The signals are then processed in the brain and the information is fed-forward to either a reproductive physiology axis (e.g., hypothalamus → pituitary → gonads and other endocrine glands) or mating behavior axis (choice or advertisement; thalamus → telencephalon → descending to brainstem and spinal cord motor areas → musculoskeletal system), which then subsequently influence reproductive state or mating behavior, respectively (Figure 37.3). On one extreme, the two domains could be mechanistically dissociated if they were stimulated by different signals and relied on different sensory channels and brain regions that process the signals prior to being fed forward to the reproductive physiology axis that influences reproductive state (Figure 37.3A) or the mating behavior axes that influence choice or advertisement (Figure 37.3B). In many systems the same courtship signals stimulate reproductive state and mating behavior. The same peripheral sense organs are stimulated in both domains, and at least the early central processing of these signals is also shared between domains. But we have no idea of the extent to which processing of signals are shared prior to their effect on reproductive state and mating behavior (Figure 37.3C). We predict that reliance on the same courtship signals will result in some mechanistic linkage between these two domains (Ryan & Wilczynski, 2014).

The degree to which reproductive physiology and mating behaviors are associated or disassociated mechanistically can influence the degree to which evolution in one domain influences evolution in the other domain. If effects in the two domains are not associated (Figure 37.3A and B) then evolution in one domain can proceed independently of evolution in the other domain. This is the implied assumption in much of the research in reproductive behavior. Alternatively, if reproductive state and mating

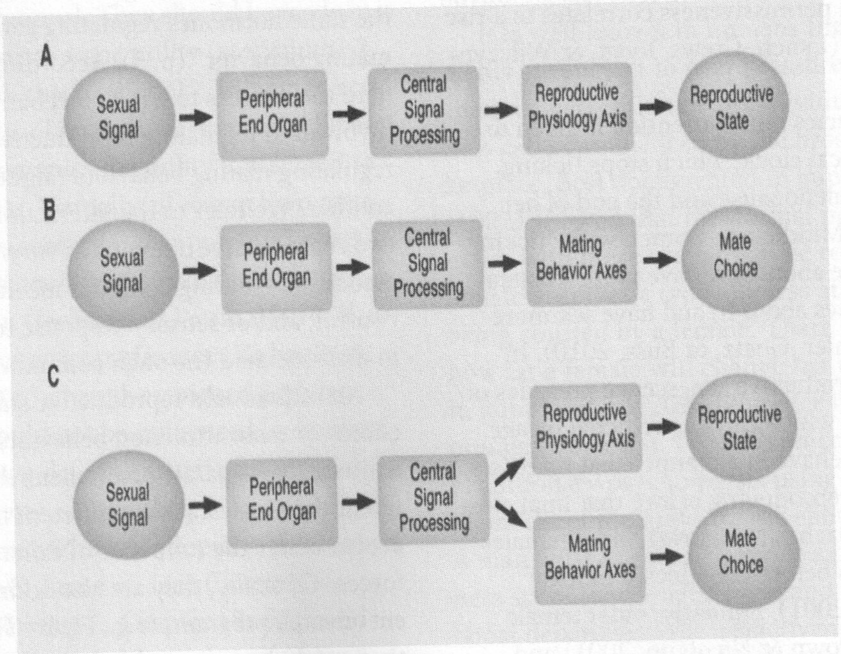

FIGURE 37.3. **Patterns of disassociation (A & B) and association (C) in the influence of signals on the domains of reproductive state and mating behaviors (mate choice in females and mate advertisement in males).**

behaviors share the same sexual signals as stimulants, and the same sensory end organs and brain regions for signal processing (i.e., if they are mechanistically associated; Figure 37.3C) then direct selection on one domain can generate indirect selection on the other domain. For example, assume that larger males with lower-frequency calls have better genes for survival. Selection will favor females who choose larger males because these females gain a fitness advantage as their offspring have higher survivorship. This could result in the evolution of spectral processing in the auditory system such that only the lower-frequency mating calls are suprathreshold and eventually elicit a mate choice. An incidental consequence or pleiotropic effect could be that only lower-frequency calls are now able to influence the female's reproductive physiology even though there was previously no fitness advantage to a female by having her reproductive state be influenced by the lower-frequency calls of larger males rather than the higher-frequency calls of smaller males.

Besides the difference in the focus of research in the domains of reproductive state (proximate concerns) and mate advertisement and choice (ultimate concerns), there is also a crucial difference in their focus on mating signals. All studies of active mate choice focus on individual differences among males in their signals. This is true by definition: If there is no signal variation, there is no basis for choice. Studies of reproductive state, however, usually focus on the species-typical signal and how this single exemplar influences reproductive state. Bentley, Wingfield, Morton, and Ball (2000) did document the surprisingly similar effects of conspecific and heterospecific song on reproductive state in domesticated canaries (*Serinus canaria domestica*) and wild white crown sparrows (*Zonotrichia leucophrys*). One of the few studies to examine signal saliency for reproductive state and mate choice is by MacDougall-Shackleton et al. (2001) who compared the saliency of natal and foreign songs of white crown sparrows. The two songs did not differ in their effect on luteinizing hormones and ovarian growth when the birds were one year of age. At two years of age, however, females were more attracted to natal calls than to foreign calls. These two studies suggest that stimulation of the reproductive axis might be more permissive than stimulating mate choice. Somewhat amazingly, the degree to which reproductive state in any animal is influenced by conspecific signal variation has not been investigated, let alone how that interaction compares to the efficacy of those same signals in mate choice.

Tinbergen (1963) codified his four questions along a proximate–ultimate dichotomy to clear up misunderstandings among those camps. But in the same paper Tinbergen suggested that we are only really interested in one question, why animals behave the way they do. In this review we have asked why animals court and choose mates as they do, and the full answers will eventually show that the proximate–ultimate dichotomy is as artificial as the other dichotomies that have gone before it.

References

Adkins-Regan, E. (2005). *Hormones and animal social behavior*. Princeton, NJ: Princeton University Press.

Akre, K. L., Farris, H. E., Lea, A. M., Page, R. A., & Ryan, M. J. (2011). Signal perception in frogs and bats and the evolution of mating signals. *Science*, *333*, 751–752. http://dx.doi.org/10.1126/science.1205623

Akre, K. L., & Johnsen, S. (2014). Psychophysics and the evolution of behavior. *Trends in Ecology and Evolution*, *29*, 291–300. http://dx.doi.org/10.1016/j.tree.2014.03.007

Alatalo, R. V., Lundberg, A., & Glynn, C. (1986). Female pied flycatchers choose territory quality and not male characteristics. *Nature*, *323*, 152–153. http://dx.doi.org/10.1038/323152a0

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Andersson, M., & Simmons, L. W. (2006). Sexual selection and mate choice. *Trends in Ecology and Evolution*, *21*, 296–302. http://dx.doi.org/10.1016/j.tree.2006.03.015

Arnqvist, G., & Nilsson, T. (2000). The evolution of polyandry: Multiple mating and female fitness in insects. *Animal Behaviour*, *60*, 145–164. http://dx.doi.org/10.1006/anbe.2000.1446

Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. http://dx.doi.org/10.1515/9781400850600

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, *2*, 349–368. http://dx.doi.org/10.1038/hdy.1948.21

Bateson, M., & Healy, S. D. (2005). Comparative evaluation and its implications for mate choice. *Trends in Ecology and Evolution*, *20*, 659–664. http://dx.doi.org/10.1016/j.tree.2005.08.013

Beecher, M. D., & Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends in Ecology and Evolution*, *20*, 143–149. http://dx.doi.org/10.1016/j.tree.2005.01.004

Bentley, G. E., Wingfield, J. C., Morton, M. L., & Ball, G. F. (2000). Stimulatory effects on the reproductive axis in female songbirds by conspecific and heterospecific male song. *Hormones and Behavior*, 37, 179–189. http://dx.doi.org/10.1006/hbeh.2000.1573

Berridge, K. C. (2007). The debate over dopamine's role in reward: The case for incentive salience. *Psychopharmacology*, *191*, 391–431. http://dx.doi.org/10.1007/s00213-006-0578-x

Billeter, J.-C., & Levine, J. D. (2013). Who is he and what is he to you? Recognition in *Drosophila melanogaster*. *Current Opinion in Neurobiology*, 23, 17–23. http://dx.doi.org/10.1016/j.conb.2012.08.009

Boughman, J. W. (2001). Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature*, *411*, 944–948. http://dx.doi.org/10.1038/35082064

Brenowitz, E. A., & Beecher, M. D. (2005). Song learning in birds: Diversity and plasticity, opportunities and challenges. *Trends in Neurosciences*, 28, 127–132. http://dx.doi.org/10.1016/j.tins.2005.01.004

Bronson, F. H. (1989). *Mammalian reproductive biology*. Chicago, IL: University of Chicago Press.

Burley, N. (1985). The organization of behavior and the evolution of sexually selected traits. *Ornithological Monographs*, 37, 22–44.

Catchpole, C. K., & Slater, P. J. (2003). *Bird song: biological themes and variations*. Cambridge, England: Cambridge University Press.

Cheng, M.-F. (2008). The role of vocal self-stimulation in female responses to males: Implications for state-reading. *Hormones and Behavior*, *53*, 1–10. http://dx.doi.org/10.1016/j.yhbeh.2007.08.007

Cohen, J. (1984). Sexual selection and the psychophysics of female choice. *Zeitschrift für Tierpsychologie*, *64*, 1–8. http://dx.doi.org/10.1111/j.1439-0310.1984.tb00348.x

Culumber, Z. W., Fisher, H. S., Tobler, M., Mateos, M., Barber, P. H., Sorenson, M. D., & Rosenthal, G. G. (2011). Replicated hybrid zones of *Xiphophorus* swordtails along an elevational gradient. *Molecular Ecology*, 20, 342–356. http://dx.doi.org/10.1111/j.1365-294X.2010.04949.x

Cummings, M. E. (2007). Sensory trade-offs predict signal divergence in Surfperch. *Evolution*, *61*, 530–545. http://dx.doi.org/10.1111/j.1558-5646.2007.00047.x

Darwin, C. (1871). *The descent of man and selection in relation to sex*. http://dx.doi.org/10.5962/bhl.title.110063

Darwin, C. (1887). *The life and letters of Charles Darwin* (F. Darwin, Ed.; Vol. 2). London, England: John Murray.

Dugatkin, L. A. (1992). Sexual selection and imitation: Females copy the mate choice of others. *American Naturalist*, *139*, 1384–1389. http://dx.doi.org/10.1086/285392

Dugatkin, L. A. (1996). Interface between culturally based preferences and genetic preferences: Female mate choice in *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, USA*, *93*, 2770–2773. http://dx.doi.org/10.1073/pnas.93.7.2770

Easton, J. A., Confer, J. C., Goetz, C. D., & Buss, D. M. (2010). Reproduction expediting: Sexual motivations, fantasies, and the ticking biological clock. *Personality and Individual Differences*, *49*, 516–520. http://dx.doi.org/10.1016/j.paid.2010.05.018

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*, 215–223. http://dx.doi.org/10.1126/science.327542

Enquist, M., & Arak, A. (1993). Selection of exaggerated male traits by female aesthetic senses. *Nature*, *361*, 446–448. http://dx.doi.org/10.1038/361446a0

Fisher, R. A. (1915). The evolution of sexual preference. *Eugenics Review*, *7*(3), 184–192.

Fisher, R. A. (1958). *The genetic theory of natural selection*. Oxford, England: Oxford University Press.

Frishkopf, L. S., Capranica, R. R., & Goldstein, M. H., Jr. (1968). Neural coding in the bullfrog's auditory system a teleological approach. *Proceedings of the IEEE*, 56, 969–980. http://dx.doi.org/10.1109/PROC.1968.6448

Garcia, C. M., & Ramirez, E. (2005). Evidence that sensory traps can evolve into honest signals. *Nature*, *434*, 501–505. http://dx.doi.org/10.1038/nature03363

Georgiadis, J. R., Kringelbach, M. L., & Pfaus, J. G. (2012). Sex for fun: A synthesis of human and animal neurobiology. *Nature Reviews Urology*, *9*, 486–498. http://dx.doi.org/10.1038/nrurol.2012.151

Gerhardt, H. C., & Huber, F. (2002). *Acoustic communication in insects and anurans*. Chicago, IL: University of Chicago Press.

Gould, J. L., Elliott, S. L., Masters, C. M., & Mukerji, J. (1999). Female preferences in a fish genus without female mate choice. *Current Biology*, *9*, 497–500. http://dx.doi.org/10.1016/S0960-9822(99)80217-6

Grant, B. R., & Grant, P. R. (2010). Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences, USA*, *107*, 20156–20163. http://dx.doi.org/10.1073/pnas.1015115107

Grant, P. R. (1972). Convergent and divergent character displacement. *Biological Journal of the Linnean Society of London*, *4*, 39–68. http://dx.doi.org/10.1111/j.1095-8312.1972.tb00690.x

Grant, P. R., & Grant, B. R. (1992). Hybridization of bird species. *Science*, *256*, 193–197. http://dx.doi.org/10.1126/science.256.5054.193

Gray, D. A. (1999). Intrinsic factors affecting female choice in house crickets: Time cost, female age, nutritional condition, body size, and size-relative reproductive investment. *Journal of Insect Behavior*, *12*, 691–700. http://dx.doi.org/10.1023/A:1020983821436

Grob, B., Knapp, L. A., Martin, R. D., & Anzenberger, G. (1998). The major histocompatibility complex and mate choice: Inbreeding avoidance and selection of good genes. *Experimental and Clinical Immunogenetics*, *15*, 119–129. http://dx.doi.org/10.1159/000019063

Gwynne, D. T. (1984). Nuptial feeding behaviour and female choice of mates in *Harpobittacus similis* (*Mecoptera: Bittacidae*). *Australian Journal of Entomology*, *23*, 271–276. http://dx.doi.org/10.1111/j.1440-6055.1984.tb01960.x

Halfwerk, W., Jones, P. L., Taylor, R. C., Ryan, M. J., & Page, R. A. (2014). Risky ripples allow bats and frogs to eavesdrop on a multisensory sexual display. *Science*, *343*, 413–416. http://dx.doi.org/10.1126/science.1244812

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, *218*, 384–387. http://dx.doi.org/10.1126/science.7123238

Han, C. S., & Jablonski, P. G. (2010). Male water striders attract predators to intimidate females into copulation. *Nature Communications*, *1*, 52. http://dx.doi.org/10.1038/ncomms1051

Hanson, H. M. (1959). Effects of discrimination training on stimulus generalization. *Journal of Experimental Psychology*, *58*, 321–334. http://dx.doi.org/10.1037/h0042606

Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences, USA, 100*, 13390–13395. http://dx.doi.org/10.1073/pnas.2333262100

Hebets, E. A., Vink, C. J., Sullivan-Beckers, L., & Rosenthal, M. F. (2013). The dominance of seismic signaling and selection for signal complexity in *Schizocosa* multimodal courtship displays. *Behavioral Ecology and Sociobiology*, *67*, 1483–1498. http://dx.doi.org/10.1007/s00265-013-1519-4

Higham, J. P., & Hebets, E. A. (2013). An introduction to multimodal communication. *Behavioral Ecology and Sociobiology*, *67*, 1381–1388. http://dx.doi.org/10.1007/s00265-013-1590-x

Hoke, K. L., Burmeister, S. S., Fernald, R. D., Rand, A. S., Ryan, M. J., & Wilczynski, W. (2004). Functional mapping of the auditory midbrain during mate call reception. *Journal of Neuroscience*, *24*, 11264–11272. http://dx.doi.org/10.1523/JNEUROSCI.2079-04.2004

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society*, *72*, 283–327. http://dx.doi.org/10.1017/S0006323196005014

Johnco, C., Wheeler, L., & Taylor, A. (2010). They do get prettier at closing time: A repeated measures study of the closing-time effect and alcohol. *Social Influence*, 5, 261–271. http://dx.doi.org/10.1080/15534510.2010.487650

Jones, A. G., Rosenqvist, G., Berglund, A., Arnold, S. J., & Avise, J. C. (2000). The Bateman gradient and the cause of sexual selection in a sex-role-reversed pipefish. *Proceedings of the Royal Society: Series B, Biological Sciences*, *267*, 677–680. http://dx.doi.org/10.1098/rspb.2000.1055

Jordan, L., Maguire, S., Hofmann, H., & Kohda, M. (in press). The over-extended phenotype: Social and ecological consequences of increased attractiveness in a social cichlid. *Proceedings of the Royal Society: Series B, Biological Sciences*.

Jordan, L. A., Kokko, H., & Kasumovic, M. M. (2014). Reproductive foragers: Spider males choose mates by selecting among competitive environments. *American Naturalist*, *183*, 638–649. http://dx.doi.org/10.1086/675755

Kirkpatrick, M., & Barton, N. H. (1997). The strength of indirect selection on female mating preferences. *Proceedings of the National Academy of Sciences, USA, 94*, 1282–1286. http://dx.doi.org/10.1073/pnas.94.4.1282

Kirkpatrick, M., Rand, A. S., & Ryan, M. J. (2006). Mate choice rules in animals. *Animal Behaviour*, *71*, 1215–1225. http://dx.doi.org/10.1016/j.anbehav.2005.11.010

Kirkpatrick, M., & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature*, *350*, 33–38. http://dx.doi.org/10.1038/350033a0

Kodric-Brown, A., & Nicoletto, P. F. (2001). Age and experience affect female choice in the guppy (*Poecilia reticulata*). *American Naturalist*, *157*, 316–323. http://dx.doi.org/10.1086/319191

Kolm, N., Amcoff, M., Mann, R. P., & Arnqvist, G. (2012). Diversification of a food-mimicking male ornament via sensory drive. *Current Biology*, *22*, 1440–1443. http://dx.doi.org/10.1016/j.cub.2012.05.050

Kraak, S. B. M., & Bakker, T. C. M. (1998). Mutual mate choice in sticklebacks: Attractive males choose big females, which lay big eggs. *Animal Behaviour*, *56*, 859–866. http://dx.doi.org/10.1006/anbe.1998.0822

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences, USA, 78*, 3721–3725. http://dx.doi.org/10.1073/pnas.78.6.3721

Lebas, N. R., & Hockham, L. R. (2005). An invasion of cheats; the evolution of worthless nuptial gifts. *Current Biology*, *15*, 64–67.

LeBlanc, M. M., Goode, C. T., MacDougall-Shackleton, E. A., & Maney, D. L. (2007). Estradiol modulates brainstem catecholaminergic cell groups and projections to the auditory forebrain in a female songbird. *Brain Research*, *1171*, 93–103. http://dx.doi.org/10.1016/j.brainres.2007.06.086

Lehrman, D. S. (1996). Interaction between internal and external environments in the regulation of the reproductive cycle of the ring dove. *Foundation of animal behavior: Classic papers with commentaries* (pp. 440–465). Chicago, IL: University of Chicago Press.

Lorenz, K., & Taylor, R. (1977). *Behind the mirror: A search for a natural history of human knowledge.* London, England: Methuen.

Lorenz, K., & Tinbergen, N. (1970). Taxis and instinctive behavior pattern in egg-rolling by the Greylag goose. *Studies in animal and human behavior* (Vol. 1, pp. 316–359). Cambridge, MA: Harvard University Press.

Lynch, K. S., Crews, D., Ryan, M. J., & Wilczynski, W. (2006). Hormonal state influences aspects of female mate choice in the Túngara Frog (*Physalaemus pustulosus*). *Hormones and Behavior*, *49*, 450–457. http://dx.doi.org/10.1016/j.yhbeh.2005.10.001

Lynch, K. S., Diekamp, B., & Ball, G. F. (2008). Catecholaminergic cell groups and vocal communication in male songbirds. *Physiology and Behavior*, *93*, 870–876. http://dx.doi.org/10.1016/j.physbeh.2007.12.004

Lynch, K. S., Rand, A. S., Ryan, M. J., & Wilczynski, W. (2005). Plasticity in female mate choice associated with changing reproductive states. *Animal Behaviour*, *69*, 689–699. http://dx.doi.org/10.1016/j.anbehav.2004.05.016

Lynch, K. S., & Wilczynski, W. (2008). Reproductive hormones modify reception of species-typical communication signals in a female anuran. *Brain, Behavior and Evolution*, *71*, 143–150. http://dx.doi.org/10.1159/000111460

Lynn, S. K., Cnaani, J., & Papaj, D. R. (2005). Peak shift discrimination learning as a mechanism of signal evolution. *Evolution*, *59*, 1300–1305. http://dx.doi.org/10.1111/j.0014-3820.2005.tb01780.x

MacDougall-Shackleton, S. A., MacDougall-Shackleton, E. A., & Hahn, T. P. (2001). Physiological and behavioural responses of female mountain white-crowned sparrows to natal-and foreign-dialect songs. *Canadian Journal of Zoology*, *79*, 325–333. http://dx.doi.org/10.1139/z00-207

Magnus, D. (1958). Exerimentelle Untersuchungen zur Bionomie und Ethologie des aisermantels *Argynnis paphia* Girard (Lep. Nymph.) [Experimental studies on the ecology and economy of the emperor mantels *Argynnis paphia* Girard (Lep. Nymph.)]. *Zeitschrift für Tierpsychologie*, *15*, 397–426.

Maney, D. L. (2013). The incentive salience of courtship vocalizations: Hormone-mediated "wanting" in the auditory system. *Hearing Research*, *305*, 19–30. http://dx.doi.org/10.1016/j.heares.2013.04.011

Marler, P. (1976). An ethological theory of the origin of vocal learning. *Annals of the New York Academy of Sciences*, *280*, 386–395. http://dx.doi.org/10.1111/j.1749-6632.1976.tb25503.x

Marler, P. (1997). Three models of song learning: Evidence from behavior. *Journal of Neurobiology*, *33*, 501–516. http://dx.doi.org/10.1002/(SICI)1097-4695(19971105)33:5<501::AID-NEU2>3.0.CO;2-8

McGurk, H., & MacDonald, J. (1976). Hearing lips and seeing voices. *Nature*, *264*, 746–748. http://dx.doi.org/10.1038/264746a0

Miller, G. F. (1998). How mate choice shaped human nature: A review of sexual selection and human evolution. In C. Crawford and D. L. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 87–129). New York, NY: Psychology Press.

Møller, A. P., & Alatalo, R. V. (1999). Good-genes effects in sexual selection. *Proceedings of the Royal Society: Series B, Biological Sciences, 266*, 85–91. http://dx.doi.org/10.1098/rspb.1999.0607

Moore, P. J., & Moore, A. J. (2001). Reproductive aging and mating: The ticking of the biological clock in female cockroaches. *Proceedings of the National Academy of Sciences, USA, 98*, 9171–9176. http://dx.doi.org/10.1073/pnas.161154598

Nakano, R., Takanashi, T., Skals, N., Surlykke, A., & Ishikawa, Y. (2010). Ultrasonic courtship songs of male Asian corn borer moths assist copulation attempts by making the females motionless. *Physiological Entomology*, *35*, 76–81. http://dx.doi.org/10.1111/j.1365-3032.2009.00712.x

O'Loghlen, A., & Rothstein, S. (2010). Multimodal signalling in a songbird: Male audiovisual displays vary significantly by social context in brown-headed cowbirds. *Animal Behaviour*, *79*, 1285–1292. http://dx.doi.org/10.1016/j.anbehav.2010.03.001

Penn, D. J., & Potts, W. K. (1999). The evolution of mating preferences and major histocompatibility complex genes. *American Naturalist, 153*, 145–164. http://dx.doi.org/10.1086/303166

Pennebaker, J., Dyer, M., Caulkins, R., Litowitz, D., Ackreman, P., Anderson, D., & McGraw, K. (1979). Don't the girls get prettier at closing time: A country and western application to psychology. *Personality and Social Psychology Bulletin, 5*, 122–125. http://dx.doi.org/10.1177/014616727900500127

Preininger, D., Boeckle, M., Freudmann, A., Starnberger, I., Sztatecsny, M., & Hödl, W. (2013). Multimodal signaling in the Small Torrent Frog (*Micrixalus saxicola*) in a complex acoustic environment. *Behavioral Ecology and Sociobiology, 67*, 1449–1456. http://dx.doi.org/10.1007/s00265-013-1489-6

Riebel, K., Naguib, M., & Gil, D. (2009). Experimental manipulation of the rearing environment influences adult female zebra finch song preferences. *Animal Behaviour, 78*, 1397–1404. http://dx.doi.org/10.1016/j.anbehav.2009.09.011

Robinson, G. E. (2004). Genomics. Beyond nature and nurture. *Science, 304*, 397–399. http://dx.doi.org/10.1126/science.1095766

Rodd, F. H., Hughes, K. A., Grether, G. F., & Baril, C. T. (2002). A possible nonsexual origin of mate preference: Are male guppies mimicking fruit? *Proceedings of the Royal Society: Series B, Biological Sciences, 269*, 475–481. http://dx.doi.org/10.1098/rspb.2001.1891

Rosenzweig, M. R., Leiman, A. L., & Breedlove, S. M. (1996). *Biological psychology*. Sunderland, MA: Sinauer.

Rowe, L., & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society: Series B, Biological Sciences, 263*, 1415–1421. http://dx.doi.org/10.1098/rspb.1996.0207

Royle, N. J., Lindström, J., & Metcalfe, N. B. (2008). Context-dependent mate choice in relation to social composition in green swordtails *Xiphophorus helleri*. *Behavioral Ecology, 19*, 998–1005. http://dx.doi.org/10.1093/beheco/arn059

Ryan, M., & Wilczynski, W. (2014). *Where the reproductive axis intersects with mate choice*. Unpublished manuscript.

Ryan, M. J. (1997). Sexual selection and mate choice. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (4th ed., pp. 179–202). Oxford, England: Blackwell.

Ryan, M. J., Bernal, X. E., & Rand, A. S. (2010). Female mate choice and the potential for ornament evolution in túngara frogs *Physalaemus pustulosus*. *Current Zoology, 56*, 343–357.

Ryan, M. J., & Cummings, M. E. (2013). Perceptual biases and mate choice. *Annual Review of Ecology Evolution and Systematics, 44*, 437–459. http://dx.doi.org/10.1146/annurev-ecolsys-110512-135901

Ryan, M. J., Fox, J. H., Wilczynski, W., & Rand, A. S. (1990). Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature, 343*, 66–67. http://dx.doi.org/10.1038/343066a0

Schiestl, F. P., Ayasse, M., Paulus, H. F., Löfstedt, C., Hansson, B. S., Ibarra, F., & Francke, W. (1999). Orchid pollination by sexual swindle. *Nature, 399*, 421. http://dx.doi.org/10.1038/20829

Schlinger, B. A., Barske, J., Day, L., Fusani, L., & Fuxjager, M. J. (2013). Hormones and the neuromuscular control of courtship in the golden-collared manakin (*Manacus vitellinus*). *Frontiers in Neuroendocrinology, 34*, 143–156. http://dx.doi.org/10.1016/j.yfrne.2013.04.001

Seehausen, O., Terai, Y., Magalhaes, I. S., Carleton, K. L., Mrosso, H. D., Miyagi, R., . . . Okada, N. (2008). Speciation through sensory drive in cichlid fish. *Nature, 455*, 620–626. http://dx.doi.org/10.1038/nature07285

Smadja, C., & Butlin, R. K. (2009). On the scent of speciation: The chemosensory system and its role in premating isolation. *Heredity, 102*, 77–97. http://dx.doi.org/10.1038/hdy.2008.55

Staddon, J. E. R. (1975). A note on evolutionary significance of supernormal stimuli. *American Naturalist, 109*, 541–545. http://dx.doi.org/10.1086/283025

Starnberger, I., Preininger, D., & Hödl, W. (2014). From uni- to multimodality: Towards an integrative view on anuran communication. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 200*, 777–787. http://dx.doi.org/10.1007/s00359-014-0923-1

Stevens, S. (1975). *Psychophysics: Introduction to its perceptual, neural, and social prospects*. New Brunswick, NJ: Transaction.

Sweeney, L. B., & Kelley, D. B. (2014). Harnessing vocal patterns for social communication. *Current Opinion in Neurobiology, 28*, 34–41. http://dx.doi.org/10.1016/j.conb.2014.06.006

Tabata, J., & Ishikawa, Y. (2005). Genetic basis to divergence of sex pheromones in two closely related moths, *Ostrinia scapulalis* and *O. zealis*. *Journal of Chemical Ecology, 31*, 1111–1124. http://dx.doi.org/10.1007/s10886-005-4251-3

Taylor, R. C., & Ryan, M. J. (2013). Interactions of multisensory components perceptually rescue túngara frog mating signals. *Science, 341*, 273–274. http://dx.doi.org/10.1126/science.1237113 ten Cate, C., & Rowe, C. (2007). Biases in signal evolution: Learning makes a difference. *Trends in Ecology and Evolution*, *22*, 380–387. http://dx.doi.org/10.1016/j.tree.2007.03.006

ten Cate, C., Verzijden, M. N., & Etman, E. (2006). Sexual imprinting can induce sexual preferences for exaggerated parental traits. *Current Biology*, *16*, 1128–1132. http://dx.doi.org/10.1016/j.cub.2006.03.068

Thornhill, R. (1976). Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (*Insecta: Mecoptera*). *American Naturalist*, *110*, 529–548. http://dx.doi.org/10.1086/283089

Tinbergen, N. (1963). On aims and methods in ethology. *Zeitschrift für Tierpsychologie*, *20*, 410–433. http://dx.doi.org/10.1111/j.1439-0310.1963.tb01161.x

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 137–180). Chicago, IL: Transaction.

Verzijden, M. N., & ten Cate, C. (2007). Early learning influences species assortative mating preferences in Lake Victoria cichlid fish. *Biology Letters*, *3*, 134–136. http://dx.doi.org/10.1098/rsbl.2006.0601

Wade, J. (2012). Sculpting reproductive circuits: Relationships among hormones, morphology and behavior in anole lizards. *General and Comparative Endocrinology*, *176*, 456–460. http://dx.doi.org/10.1016/j.ygcen.2011.12.011

Waynforth, D. (2007). Mate choice copying in humans. *Human Nature*, *18*, 264–271. http://dx.doi.org/10.1007/s12110-007-9004-2

Wedekind, C., & Füri, S. (1997). Body odour preferences in men and women: Do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society: Series B, Biological Sciences, 264*, 1471–1479. http://dx.doi.org/10.1098/rspb.1997.0204

Wilczynski, W., & Ryan, M. J. (2010). The behavioral neuroscience of anuran social signal processing. *Current Opinion in Neurobiology*, *20*, 754–763. http://dx.doi.org/10.1016/j.conb.2010.08.021

Wilkinson, G. S., & Reillo, P. R. (1994). Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society: Series B, Biological Sciences*, *255*, 1–6. http://dx.doi.org/10.1098/rspb.1994.0001

Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*, 829–846. http://dx.doi.org/10.1086/285134

Woolley, S. M. (2012). Early experience shapes vocal neural coding and perception in songbirds. *Developmental Psychobiology*, *54*, 612–631. http://dx.doi.org/10.1002/dev.21014

Zahavi, A. (1975). Mate selection-a selection for a handicap. *Journal of Theoretical Biology*, *53*, 205–214. http://dx.doi.org/10.1016/0022-5193(75)90111-3