



# Mate Choice and Mating Preferences

## AN OVERVIEW

### 1.1 INTRODUCTION

Hiking in the eucalyptus woods of northern Australia, we might come upon an odd structure with a promenade of shells and bones leading up to a curving, symmetric arch. We might reasonably speculate that we have stumbled upon an indigenous ceremonial site, or perhaps a contemporary art installation (fig. 1.1a). Diving off Japan's Okinawa Prefecture, we come upon a similar structure—an “alien crop circle” in the popular media (fig. 1.1b). We are astonished when we discover that the architects were a male great bowerbird (*Ptilonorhynchus nuchalis*) and a male pufferfish (*Torquigener* sp.), and that these structures only function in the context of courtship and mating. As amazed as we are by the structures' builders, we should be awestruck by the aesthetics of the females they were built to impress. How intricate their aesthetics, how exacting their desires, must be in order to drive males to such cognitive and physical extremes? Why do females even bother to choose males on the basis of these structures, rather than simply mating at random?

Mating is an expensive, risky, and intimate interaction, and over an individual's lifetime one expends time and energy on facilitating some matings, and time and energy on avoiding others. Who a **chooser**<sup>1</sup> mates with and who she pairs with will affect how long she lives and how many healthy children and grandchildren she has. Mate choice determines which sperm fuse with which eggs, and therefore ultimately shapes how lineages split apart or merge together. It can drive the evolution of elaborate traits that hinder critical tasks like finding food and avoiding predators, in direct opposition to **natural selection**. The role of mate choice in both **reproductive isolation** among species and in **sexual selection** made it a key concept in Darwin's *Origin of Species* (1859). There was widespread skepticism over his conjecture that mating **preferences**—a “taste for the beautiful,” in Darwin's

<sup>1</sup> Boldfaced terms are defined in the glossary.

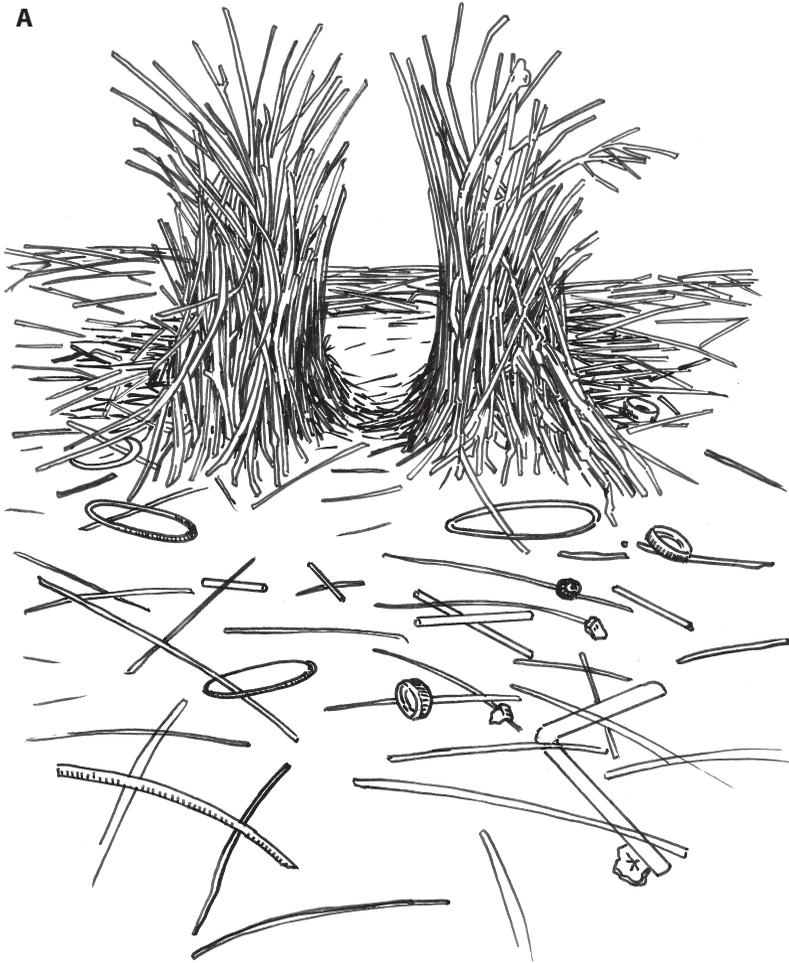
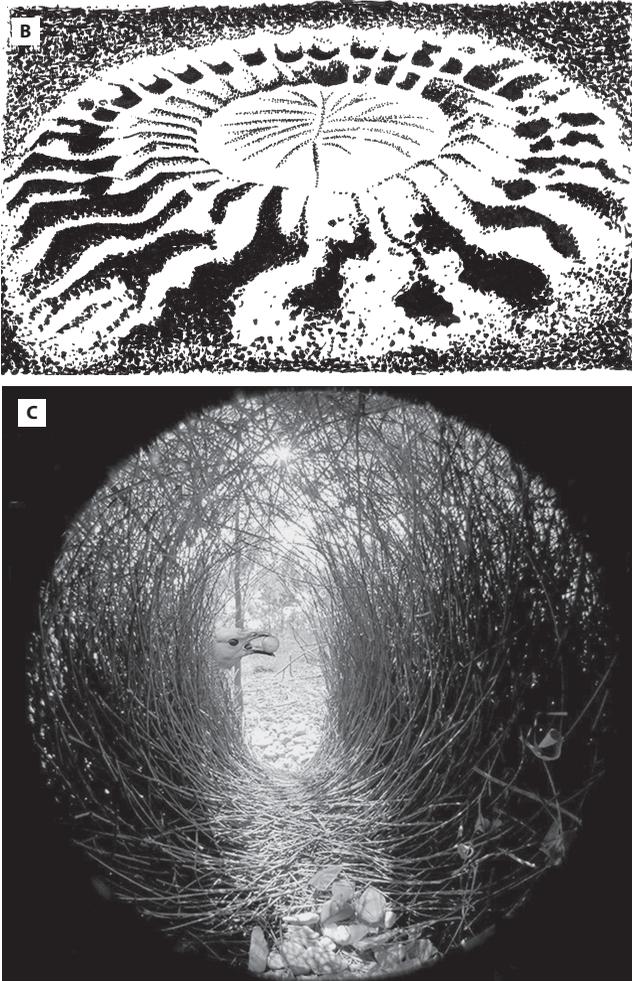


Figure 1.1. (a) Bower of a satin bowerbird, *Ptilonorhynchus violaceus*, Queen Mary Falls, Queensland, Australia. Drawing from photo by Gail Patricelli.

memorable phrasing—could explain the seeming paradox of so much exuberant scent, texture, and sound in nature. Accordingly, he devoted the bulk of his next major work, *The Descent of Man, and Selection in Relation to Sex* (1871), to making the case for the central evolutionary role of sexual selection, particularly via mate choice.

Almost a century and a half later, mate choice continues to present a unique problem in evolutionary theory. Like predators coevolving with their prey, or hosts with their parasites, those courting and those choosing form



(b) Bower of a pufferfish, *Torquigener* sp., off Okinawa prefecture, Japan (Kawase et al. 2013). (c) Composite image of a displaying male great bowerbird (*P. nuchalis*) and bower as it appears to a choosing female, © 2017 John Endler.

a feedback loop, where **chooser** decisions can select for particular **courter** behavior and vice versa. In the case of mate choice, however, the same genome influences the behavior of both actors, and the interests of both are partly aligned and partly in conflict (Arnqvist & Rowe 2005). This kind of dynamic can lead to rapid evolution of elaboration of signals and choices within a species, which can lead to marked diversity of such signals and choices between species. Such divergent mate-choice patterns are often a

prerequisite for reproductive barriers among species. Both the formation of new species, and the blending together of species via hybridization, depend on individual mate-choice decisions.

The study of mate choice is both fueled and complicated by its importance to our everyday experience. Mate choice forms our human identity: we are who we are because of a chain of highly improbable reproductive decisions, and our lives are in no small part defined by the people we desire, those with whom we have sexual relationships, and those with whom we reproduce. Our decisions to do so are regulated, to varying degrees in different times and places, by families, communities, and governments; few things are more painful than having our choices thwarted or overridden. It is hard to imagine music, prose, and poetry without love, jealousy, or heartache. And when we court each other and choose each other by starlight, we do so to the soundtrack of crickets and frogs doing the same. Mate choice surrounds us.

It is easy to make the case that mate choice is important, but how it actually evolves and how it actually works remains essentially mysterious. We are at a loss to explain much of the beauty in the world, from birdsong to the palette of colors on a coral reef, because we know that these things arise from mate choice, but we are still striving to understand how. We don't understand why choosers pay attention to so many different things or how they integrate information into a unitary decision to mate. Perhaps most visibly, we still fail to agree on the importance of **adaptive** processes in mate choice. My first scholarly exposure to mate choice was in the fall of 1993, in a freshman seminar on "Sex and Evolution" led by Jae Choe. At the time, the field was consumed by a debate about the extent to which an individual's mate-choice decisions impact the "genetic quality" of her offspring. Two decades later, we remain mired in, and limited by, the argument of whether or not mate choice is optimally designed to pick mates bearing "good genes."

There are at least three reasons why the conversation hasn't changed much over a generation. The first reason is that work on mate choice is hard to do; the core of mate-choice research involves inferring and predicting mating decisions indirectly and/or over long timescales. This is because mate choice as a phenotype is inherently slippery; we're usually measuring behavioral decisions, which are inherently contingent on the stimuli presented, and can only be measured indirectly. We can readily measure the spectral reflectance of the components of a bower and calculate how they catch the sunlight over the course of a day, but it's much more challenging to measure how these components influence the likelihood that a female will

mate with the male who produced it. The next chapter deals with the technical challenges of measuring mate choice.

The second reason is the Balkanization of our approaches to studying mate choice. Those who study humans are generally associated with entirely different disciplines (anthropology and social and evolutionary psychology) than the majority of their colleagues working on non-humans (biology and its subfields, as well as comparative psychology). Biologists, moreover, are further subdivided into quantitative geneticists, behavioral ecologists, ethologists, and behavioral neuroscientists. The massive literature on mate choice is a mixed blessing, since it makes it difficult for any individual to have in-depth knowledge of more than one of these areas. A major goal of this book is to bring these fields together toward a synthetic understanding of mate choice.

The third and perhaps principal reason for the field's slow progress is that we have always thought about mate choice primarily in terms of its functional *consequences*. Starting with Darwin (*The Descent of Man, and Selection in Relation to Sex*, 1871) and sexual psychologist Havelock Ellis (*Sexual Selection in Man*, 1905), and continuing on to the present (Andersson, *Sexual Selection*, 1994; Eberhard, *Female Control: Sexual Selection by Female Choice*, 1996; Arnqvist & Rowe, *Sexual Conflict*, 2005), the focus has not been on mate choice as an intricate psychological and behavioral process in its own right, but on mate choice as an agent of sexual selection. Evolutionary models sometimes rely on fanciful assumptions about mechanisms; conversely, empirical studies of mechanism frequently assume optimal design. Conversely, to the extent that those who study mate-choice mechanisms think about **fitness** consequences, they often assume these mechanisms are systems optimally designed to maximize the benefits of mate choice to choosers, rather than systems cobbled together from available genetic variation that sometimes lead choosers astray. It is tempting to think of choosers as actuaries, evaluating expected lifetime fitness, and taxonomists, recognizing **conspecifics** and **heterospecifics**, and executing each of these tasks both perfectly and separately. Yet relatively little attention is paid to how mate choice actually works, although this is crucial to understanding both how it evolves and how it imposes selection. How does a female bowerbird actually experience her choices (fig. 1.1c)? Our focus on courter traits, rather than chooser preferences, has produced some stumbling blocks for evolutionary theory: one important example is that the predictions of most sexual selection models depend entirely on whether the net direct benefits of mate choice are positive or negative, yet we seldom measure this directly.

What is **total selection on mate choice**, and how does it affect the way preferences and sampling strategies evolve?

The standard approach in the mate-choice literature is to begin by reviewing theoretical and conceptual models, then discussing empirical evidence in light of the theory. Inspired by Darwin's inductive approach in the *Origin* and the *Descent*, I have attempted to turn this approach upside down and interpret theory in light of what we know about how mate choice works. Accordingly, I focus this first section of the book on natural history—a broad description of the mechanisms, ontogeny, and phenotypic expression of mating preferences and mate choice. I have deliberately chosen my language to minimize a priori assumptions about any adaptive functions of choosing particular mates over others. In the second section, I use this perspective to address how mate choice evolves and acts as an agent of selection, and how it generates fitness consequences for individuals and evolutionary consequences for populations and species.

Part of the challenge of studying mate choice arises from the enormous scope of mate choice as a phenomenon. The contemporary literature on mate choice is immense. Choice can range from the simplicity of a single-celled protozoan exchanging genes only with another individual emitting a particular signaling molecule, through the protracted mutual courtship of humans and other vertebrates. What these vastly different mechanisms have in common is that they impose variation in the mating success of the *individuals being chosen*—courtiers. Preferred courtiers will, by definition, have an advantage over unpreferred ones (but see Long et al. 2009 for a counterexample).

By contrast, the magnitude and direction of mate choice's benefits to *choosers* is hugely variable, and while sophisticated mate-choice mechanisms offer more opportunity for nuanced **evaluation** and comparison, they also offer greater entry for subversion and deceit. Some of the mechanisms involved in mate choice, like the tuning of peripheral sensory receptors, are universal among organisms. Other mechanisms, such as selective attention to particular traits, are highly labile among species, within species, and even within individuals. A recurring theme of this book is the importance of the processes promoting and maintaining within-population variation in mate choice.

Like the mechanisms used for mate choice, the ecological theater of mate choice spans the full range of natural history. Mate choice occurs in everything from parrots that grow up with both parents, to parrotfish that are cast off into the plankton as fertilized eggs. There is mate choice among

anglerfish in the deep ocean that encounter mates so rarely that when they do, males permanently attach to females, their circulatory systems fusing together; and there is mate choice among crickets in noisy choruses, surrounded by thousands of courters and choosers. Both the mechanisms constituting mate choice and the selective pressures shaping it are thus as variable as can be among taxa. The diversity of mate-choice mechanisms provides the potential for wonderful natural experiments, but these are again limited by the difficulties inherent in measuring choice. One person can easily go to museums and measure a morphological trait in a hundred species. An individual research lab working on mate choice can manage at most a handful of species with similar maintenance needs. Accordingly, taxonomic clustering adds to the intellectual Balkanization of mate choice. Social-context effects on mating (chapter 6) are one example. Nearly all studies of sexual reward come from one rodent species, and nearly all studies of mate-choice **copying** come from one fish family and one bird species. With different model systems come different constraints as to what we can measure, different traditions of what's important to think about, and different networks of researchers. This book attempts to bring these approaches together and survey mate choice across taxa (including humans), striving to avoid being too biased by my own inordinate fondness for livebearing fishes.

Attempts to fit mate choice between two covers are, perhaps sensibly, few and far between. Since Bateson's (1983) eponymous edited volume on mate choice, we have gained considerable ground in understanding sensory, perceptual, and cognitive mechanisms, and in understanding the evolutionary causes and consequences of choice. Across fields, the literature on mate choice has exploded. The aim of this book is to present a conceptually unified approach to thinking about what Darwin termed the "taste for the beautiful." It is not intended to be an exhaustive review of the literature, particularly since any such effort would be both redundant with the Internet and obsolete by the time of publication. I have attempted to synthesize the work of hundreds of people, but the papers I cite are probably biased by my taxonomic and geographic parochialism (Wong & Kokko 2005). I have tried to abide by the late Stephen Jay Gould's (1994, p. 164) maxim that erroneous ideas are useful, since they can invigorate science by stimulating new avenues of thought, while misleading facts are corrosive. Therefore, I have endeavored to be meticulous in terms of characterizing my sources, but have allowed myself some qualified speculation in the hopes of generating new conversations about mate choice. Nevertheless, I am a tourist to many of the subdisciplines involved, and although I have made an effort to

have each chapter read by at least one expert colleague, the book surely retains mistakes and misconceptions that are entirely my own.

In this chapter, I begin by describing a basic framework for thinking about mate choice and mate preferences, and then provide an outline for how the book attempts to address key questions about how they work, how they evolve, and how they act simultaneously as targets and agents of selection.

## 1.2 WHAT IS MATE CHOICE?

It is possible therefore that the emotional reactions aroused by different individuals of the opposite sex will, as in man, be not all alike, and at the least that individuals of either sex will be less easily induced to pair with some partners than with others. With plants an analogous means of discrimination seems to exist in the differential growth rate of different kinds of pollen in penetrating the same style.

—Fisher (1930, p. 143)

One of the challenges of learning cell biology or neuroanatomy is the sheer amount of new vocabulary it entails. Students are overwhelmed by trying to keep the anterior cingulate cortex straight from the torus semicircularis. Animal behavior, by contrast, tends to assign specialized meaning to ordinary terms: while this makes them more accessible to a broad audience, it can lead to semantic confusion and anthropomorphism. Further, different authors use myriad terms to describe comparable processes. Edward (2015) provides a comprehensive review of the terminology surrounding mate choice and mating preferences. This book is biased toward multicellular animals with neurally mediated behavior, to which some authors prefer to restrict the term “choice.” But neither sensory perception nor neural processing are required for a mechanism that discriminates among potential mates. Most contemporary scientists (Edward 2015; Kokko et al. 2003; Servedio & Bürger 2014) use variations on Halliday’s (1983, p. 4) definition, which extends mate choice to a broad range of mechanisms in even the simplest creatures:

Mate choice can be operationally defined as any pattern of behavior, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others.

The focus of this book is on neurally mediated behavior in animals, but chemically or morphologically mediated, non-neural mate choice is the only option for plants (Burley & Willson 1983) and microorganisms (e.g., Lin 2009) and plays an important role in postmating choice in animals (chapter 7). If we change “patterns of behavior” to the more general “phenotypes,” Halliday’s definition encompasses mate choice in each of these systems.

Halliday’s definition of mate choice is restricted to opposite-sex interactions. A growing number of studies (reviewed in Bagemihl 1999; Bailey & Zuk 2009b; Poiani 2010) have highlighted the ubiquity of same-sex sexual behavior across the animal kingdom; and more generally, an individual’s sexual partners (homo- or heterosexual) can influence that individual’s fitness independent of whether gametes are exchanged (chapter 14). Further, as I will argue below, “mating” is not a discrete event. I therefore suggest a modification of Halliday’s (1983) definition to take into account the possibility of same-sex partners: **mate choice** can be defined as any aspect of an animal’s phenotype that leads to its being more likely to engage in sexual activity with certain individuals than with others.

### 1.3 CHOOSERS AND COURTERS, NOT FEMALES AND MALES

Many authors use “female” and “male” as convenient shorthand for the individuals choosing and courting. This is because the distribution of potential mates is usually male-skewed, meaning there are many more males available to mate at a given time than females. Accordingly, females tend to be chooser than males. A growing body of work, however, emphasizes the role of male mate choice not only in sex-role-reversed species like pipefish and jacanas, but also in species where strong female choice is present as well. And sexual selection can act strongly on females (reviewed in Clutton-Brock 2009; chapter 8). Accordingly, I use the terms *chooser* and *courter* throughout this book. In addition to being sex- (and gender-) neutral, these terms refer to behavioral roles rather than to permanent aspects of the phenotype. Ecological circumstances like the availability of suitable territories can determine which sex chooses. In monogamous or hermaphroditic animals, the roles of courter and chooser can even reverse over the course of a single social interaction. It is therefore more productive to think about mate choice in terms of the roles that individuals are playing over the course of a given interaction.

## 1.4. MATE CHOICE IS DISTINCT FROM SEXUAL SELECTION

Mate choice has *ab ovo* been cast as the handmaiden of sexual selection:

I cannot here enter on the necessary details; but if man can in a short time give beauty and an elegant carriage to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect. (Darwin 1859)

In the *Origin* and, more extensively, in the *Descent of Man, and Selection in Relation to Sex* (1871), mate choice plays an important, novel, but ultimately supporting role in sexual selection. The superstar is the evolution of intricate songs and elaborate plumage in birds, which Darwin regarded as self-evidently “beautiful.” Darwin’s proposed agent of sexual selection was the strikingly un-Darwinian “taste for the beautiful”: slippery, anthropomorphic, mystical, and tautological. Part of the reason this hypothesis was rejected by Darwin’s contemporaries was because, uncharacteristically, he treated this taste for the beautiful as axiomatic and failed to provide a satisfying evolutionary explanation for its origin or maintenance (Cronin 1991; Milam 2010).

Darwin’s Victorian contemporaries were skeptical that animals, particularly female animals, could be capable of making aesthetic distinctions. This skepticism was of course exacerbated by the conventional sexism of Darwin’s time, but Darwin didn’t help his case by treating female cognitive inferiority as a self-evident fact of nature, and by throwing up his hands at the complexity of mate choice. As Milam (2010) points out in her excellent social history of the science of mate choice, Darwin’s implication of “love or jealousy” as agents of choice suggested that sophisticated cognitive mechanisms might be involved; indeed, Darwin (1871) argued that mate choice would be restricted to species with “powers of the mind [that] manifestly depend on the development of the brain.”

The subsequent century and a half of research on mate choice and mating preferences has largely continued Darwin’s approach of viewing preferences in light of their role as agents of selection, even as it has partly demystified mate choice and demonstrated its operation in very simple biological systems. The foundational theory of R. A. Fisher (1930) focused on courtship traits as the driver of preference evolution; the hypotheses of Zahavi (1975) further posited that these traits provided information to choosers about the genetic makeup of their offspring. The trait-centered perspectives of these

evolutionary biologists were mirrored by the work of mid-twentieth-century **ethologists**, who mainly viewed mating interactions through the lens of courters (invariably males) “priming” the sexual receptivity of their mates. This obviated the need to think about any kind of agency on the part of choosers. Yet some courters are better than others at “priming,” which allows us to think about sexual receptivity as a mechanism of mate choice (chapter 6); indeed, in the Australian redback spider, insufficiently stimulated females devour their suitors before mating occurs (Stoltz & Andrade 2010). Courters’ efforts to induce choosers to mate, and choosers’ responses to such efforts, set the stage for **sexual conflict** (chapter 15).

As will become clear throughout this book, mate-choice decisions can be adaptive, non-adaptive, or **maladaptive**, and mating preferences do not map cleanly to the traits that courters express in the real world: choosers often prefer combinations of traits that are unavailable in real courters. Mate-choice mechanisms are subject to multiple selective forces independent of the mating outcomes they shape. Conversely, strong preferences based on individual compatibility do not generate sexual selection. As Bateson (1983, p. ix) wrote in his preface to *Mate Choice*:

When the term “mate selection” is used for what animals do, it can quickly lead to unconscious punning and the assumption that a preference for a particular kind of mate necessarily has implications for sexual selection. As will become plain, the assumption is false.

## 1.5 PREFERENCE AND ANTIPATHY UNDERLIE REALIZED MATE CHOICES

### 1.5.1 Preference

To understand what Bateson meant about the study of mate choice not being about sexual selection, it is important to distinguish between “mate choice” and “mate preference.” These are sometimes thought synonymous, but they can be very different things. A **preference** is a chooser’s internal representation of courter traits that predisposes her to mate with some phenotypes over others (Heisler et al. 1987; Jennions & Petrie 1997). Cotton and colleagues (2006a) separate “preference” into preference functions (fig. 1.2, see page 16), which correspond to the preceding definition, and the process of sampling and deciding among mates. For clarity, I restrict “preference” to the narrower definition. In chapter 6, I will return to the interdependence of preferences with mate sampling and mating decisions.

Preference by definition means that choosers are influenced differently by different stimuli; it is an inherently comparative process, even though it is convenient to think about “absolute” preferences in some contexts (chapter 2). Preference can be applied to a ranking of individuals (Harry prefers Sally over Marie) or of discrete characters (female túngara frogs, *Physalaemus pustulosus*, have a preference for calls followed by short, high-energy bursts called “chucks” over those without), or to a continuous function (female swordtails, *Xiphophorus hellerii*, have a **directional** preference function for longer tails on males). Univariate and multivariate preference functions are discussed below. Crucially, preferences don’t have to be realized into choices; indeed, choosers often have strong preferences for trait values, or combinations of traits, that are unavailable in courters (Fisher et al. 2009). Such “hidden” preferences are universal and have the potential, once revealed by novel courter traits, to induce rapid and permanent evolutionary change (chapter 13).

### 1.5.2 Antipathy

We tend to think of mate choice in terms of which individuals or traits are most preferred, rather than which are rejected by choosers. Often, choosers expend more energy avoiding rejected courters than seeking out preferred ones. Even when rejection is relatively cost-free, mate choice invariably involves rejecting many more mates than one accepts; indeed, choosers may forgo mating altogether if no acceptable options are available (or, notably in flowering plants, to self-fertilize rather than mate with a different genetic individual; Burley & Willson 1983). Most preference envelopes—the space of acceptable mates—are very narrow, in the sense that there are almost always infinitely more ways that a courter can be unacceptable than acceptable. And, as Darwin recognized, choosers may often select not the most enticing available mate, but the least repulsive:

[T]he female, though comparatively passive, generally exerts some choice and accepts one male in preference to others. Or she may accept, as appearances would sometimes lead us to believe, not the male which is the most attractive to her, but the one which is the least distasteful. (1871, p. 273)

Darwin returns frequently to this point and uses the term **antipathy** to describe when a particular individual, category, or trait value is less attractive than others. The term “antipathy” has not seen wide use in the recent literature, but as I will argue throughout this book, choosers’ rejection of

unattractive courters is generally more important than their acceptance of attractive ones, because of the downside risk of inappropriate matings (Clemens et al. 2014). The literature on sexual conflict (chapter 15) often refers to **resistance** (Holland & Rice 1998). For example, in female seaweed flies, *Coelopa frigida*, a female's mate choice is manifested mostly by physical rebuffs and signals of rejection (Blyth & Gilburn 2011). Preferred males are the ones that encounter the least resistance. In birds and mammals particularly, researchers frequently measure both negative (**aversive**) and positive (**appetitive** or **proceptive**) behaviors when characterizing preferences. For example, Forstmeier and colleagues (2004) assigned positive and negative preference scores based on the observation of appetitive and aversive behaviors, respectively. The most preferred courter is thus not only the individual who elicited the most positive responses, but also the least negative responses; the most beautiful is also the least distasteful. This may not matter much to courters, but the subjective value of mating encounters—whether choosers perceive them as positive or negative experiences—can affect a chooser's future mating decisions, making them more averse or more responsive to particular courter phenotypes (chapter 6).

Mate choice, then, is the phenotypic manifestation of preference and antipathy. Realized choices are constrained by the availability of courter phenotypes, by courter actions toward choosers, and by the way that choosers sample potential mates. Mate sampling and preference functions are intertwined, in that the sampling experience can change chooser preferences (chapter 6).

## 1.6 PREFERENCE FUNCTIONS

### 1.6.1 Overview

Chooser preferences are internal representation of the properties of courter stimuli. We also apply the term “preference” rather loosely to behavioral or other measures that vary according to courter stimulus; accordingly, a common way of representing preference is to plot a chooser's response—our choice of assay—as a function of courter trait values. This is a **preference function** (Wagner 1998; fig. 1.2), in which the mating response varies with the value of a trait. Preference functions are convenient concepts in studies of sexual selection via mate choice; in the idealized case where they perfectly predict realized mate choice and are the same for all choosers in a population, they represent **fitness functions** for chooser traits (chapter 14).

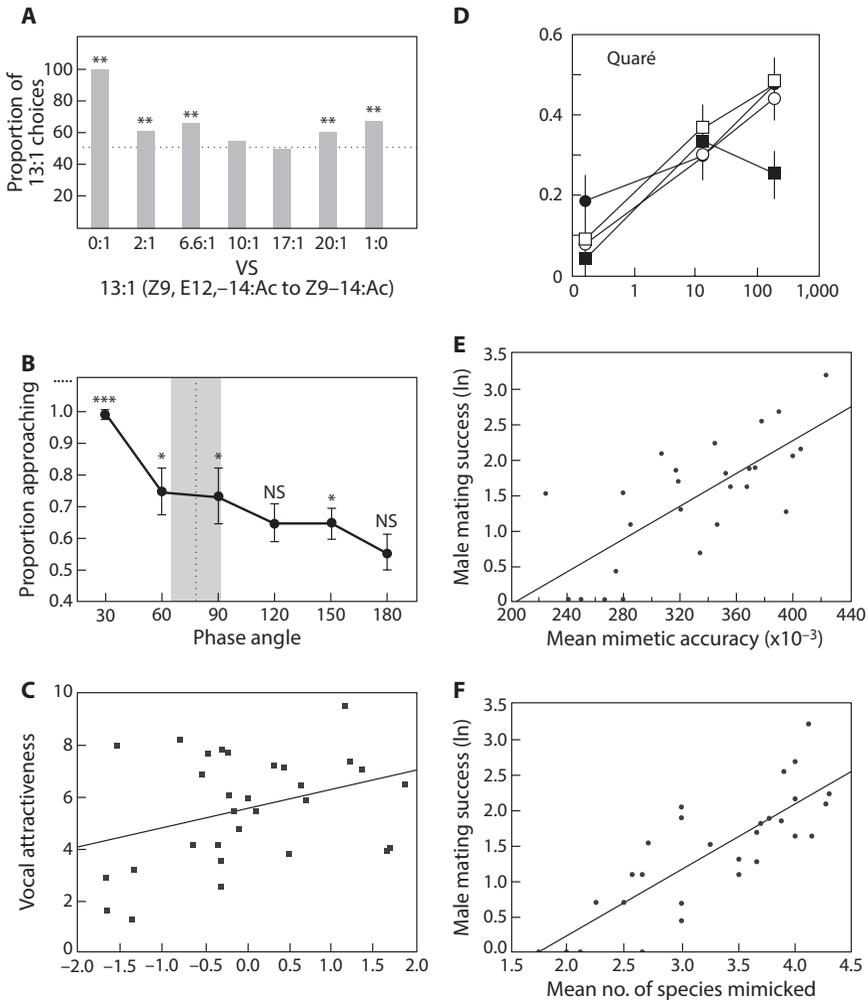


Figure 1.2. Preference functions. (a) Proportion of male almond moths orienting to the species-typical female pheromone blend when presented as an alternative to the ratio on the Y-axis (Allison & Cardé 2008); (b) approach probability of female midwife toads to the temporally leading call in a pair of stimuli presented with varying degree of temporal offset. At 30 degrees of phase angle, the leading call immediately precedes the following call; at 180 degrees, they are exactly antiphonal (Bosch & Márquez 2002); (c) Mean attractiveness rating of female voices by British men as a function of higher harmonic frequencies (Collins & Missing 2003); (d) Proportion of a male's courtship displays that elicit a "glide" sexual response from female guppies from the Quare drainage, Trinidad, as a function of dietary carotenoid concentration (ppm) and male and female population of origin (circles/squares—males from low/high carotenoid-availability streams; filled/unfilled—females from low/high streams) (Grether 2000); and mating success of male satin bowerbirds as a function of (e) the accuracy and (f) taxonomic diversity of their courtship vocalizations (Coleman et al. 2007).

The conceptual usefulness of preference functions is limited, however, when we start to consider the comparative nature of preference, whereby a stimulus's attractiveness is contingent on comparisons to other traits (chapter 6).

Preference functions represent a measure of mate choice in relation to continuous or ordinal variation in a courter trait. Measuring preference functions, by definition, requires sampling chooser responses to multiple trait values, and requires that chooser response be expressed as a continuous or ordinal variable (Wagner 1998). For empiricists, the response is typically represented as the frequency or duration of a particular behavior associated with mating (chapter 2) or as the proportion of individuals in a sample choosing a particular trait. Preference functions can either represent absolute responses to a stimulus (fig. 1.2c–f) or relative preferences between or among stimuli (fig. 1.2a–b).

Preference functions vary considerably among individuals in the same population or species (Jennions & Petrie 1997; chapter 9), which can have fundamental consequences for sexual selection (chapter 15) and speciation (chapter 16). To understand among-individual variation in mating preferences, we need to characterize preference functions for distinct individuals (Wagner 1998), which poses several challenges—notably that assaying preferences inevitably changes individual experience. Preference assays and repeated testing of individuals are discussed in the next chapter.

The **shape** (or “form”; Cotton et al. 2006) of a preference function falls into a few broad categories (Ritchie 1996; Edward 2015): **unimodal**, with choosers preferring an optimal trait value (fig. 1.3a); more rarely, **bimodal** or multimodal, where choosers prefer two or more distinct trait values (fig. 1.3b); or **directional**, where preferences increase (or decrease) monotonically with trait value (fig. 1.3c). While some preferences appear to be directional within the range of current courter phenotypes, any preference will be limited, at the very least, by minimum **thresholds** for detection at the low end of trait values, and by sensory receptor saturation or cognitive constraints at the high end (fig. 1.3d; chapter 3). Most trait values we actually measure are also physically constrained to be positive (fig. 1.3d).

Preferences may also be **categorical**, with choosers attending only to traits within a certain range of values, but distinguishing little within that range (fig. 1.3e; chapter 4). Note that categorical preferences are analogous to Edward's (2015) “threshold” preferences; I use the term *categorical* for consistency with the cognition literature (chapter 4). As noted above, continuous preference functions will always have maximum and minimum thresholds, although threshold values may be unobserved or unattainable in actual courters.

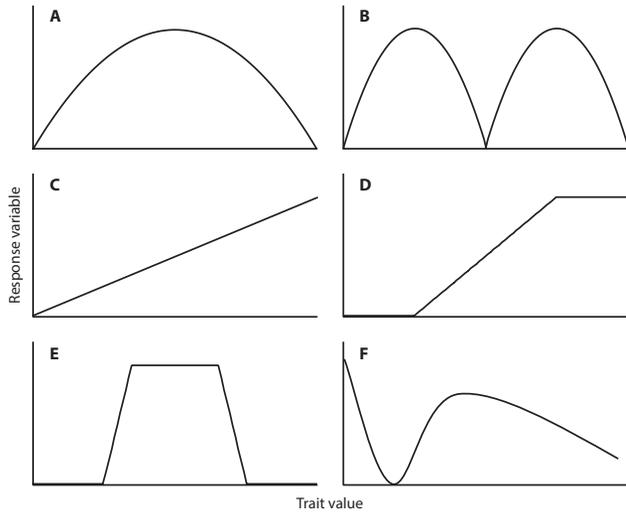


Figure 1.3. Shapes of preference functions: (a) unimodal; (b) bimodal; (c) directional; (d) sigmoid; (e) categorical; (f) complex.

Finally, preferences may be complex (fig. 1.3f). There are few examples of complex (or bimodal) preferences in mate choice, although it should be noted that we rarely have the statistical power to fit complex functions to preference measures. Mori's (1970) “**uncanny valley**,” however, is a familiar reminder that preferences can be highly nonlinear. Mori, a roboticist, was pessimistic about efforts to make robots more humanlike in morphology and behavior, because too-humanoid robots would be less appealing to humans (think *Star Wars*' creepy C3P0 versus the adorable R2D2). People, Mori argued, exhibit maximal disgust toward stimuli that are slightly dissimilar from healthy humans, notably corpses, resulting in a preference function like the one in figure 1.3f. Beyond popular culture, there has been limited work on the uncanny valley. Matsuda and colleagues (2012), however, showed that infants prefer faces of their mothers over those of unfamiliar women, while intermediate faces between the two women lie in a zone of reduced attractiveness. Karl MacDorman and colleagues have conducted a detailed series of studies of the cognitive mechanisms underlying the uncanny valley in adults (e.g., MacDorman & Chattopadhyay 2016, and references therein). If preferences are largely driven by low-level sensory responses (chapter 3), they will generally be directional or unimodal in shape (Ryan & Keddy-Hector 1992), whereas integration of multiple cues may result in categorical or complex preferences (chapters 4 and 5).

It is useful to extract summary measures from preference functions that correspond to biologically meaningful properties of chooser behavior. These

parameters are referred to by different names by different authors; for example, the term “strength of preference” has been variously used to discuss each of the first three properties described below: peak preference, responsiveness, and choosiness. For simplicity’s sake, I use these terms throughout this book when characterizing preferences.

### 1.6.2 Peak preference

The **peak preference** (fig. 1.4a) is the trait value that elicits the maximum response from choosers. Peak preference corresponds to the “ideal point” in political science and economics (Poole 2005). If preferences are multi-modal or complex, it makes sense to identify local maxima; that is, multiple peaks within a preference function.

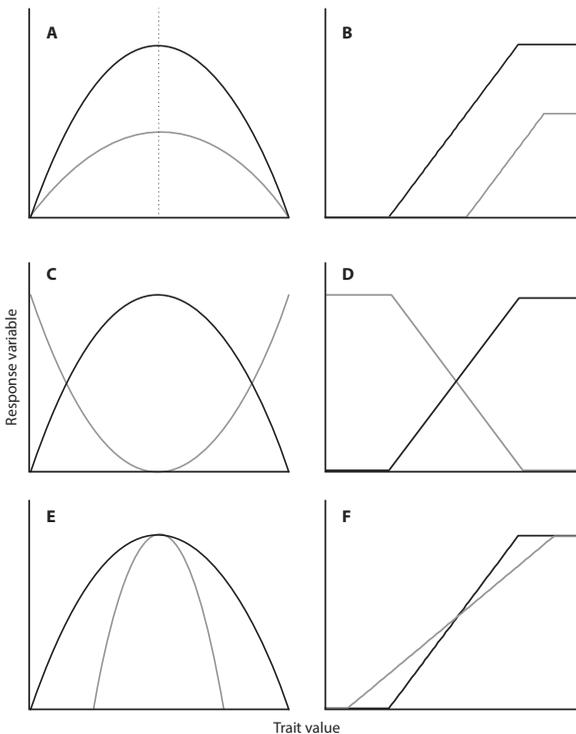


Figure 1.4. Properties of preference functions. Dashed line in (a) indicates peak preference. Black and gray preference functions in (a) and (b) differ in responsiveness; preference functions in (c) and (d) differ in valence; in (e) and (f), in choosiness.

### 1.6.3 Valence

The term **valence** has not seen wide use in the literature, but genotype, social experience, and environmental effects can all act to flip the direction of preference—that is, preference versus antipathy. For example, female Gouldian finches (*Erythrura gouldiae*) show Z-linked reversals in preference for male color morph (Pryke 2010) and male zebra finches (*Taeniopygia guttata*) show experience-dependent reversals in preference for bill color (fig. 1.4c–d). Both guppies (*Poecilia reticulata*, Endler & Houde 1995) and great bowerbirds (*P. nuchalis*) show preferences for some colors and antipathy for others. Variation in the direction of preference is important to distinguish from variation in preference function or preference shape, since shifts in preference direction can lead to rapid evolution and diversification of courter traits. Valence is explored in detail in chapter 5.

### 1.6.4 Responsiveness

**Responsiveness** (fig. 1.4a–b; Brooks & Endler 2001) is the chooser response averaged over the distribution of a courter trait in a specified reference population, whether based on natural variation or on the values determined by the experimenter. Responsiveness corresponds to the motivation to mate, which in turn often depends on physiological receptivity (chapter 6). Responsiveness is particularly important in the context of sexual conflict (chapter 15), since it can evolve in response to courter signals that impose costs on choosers. Resistance (Holland & Rice 1998) is essentially the inverse of responsiveness (Rosenthal & Servedio 1999); a chooser with the gray preference function in figure 1.4a has lower responsiveness and higher resistance to courter traits than a chooser with the black preference function.

### 1.6.4 Choosiness

A crucial but more complicated property of preference functions is **choosiness**, conceptually defined as “time or effort that [a chooser] is prepared to invest in making a choice” (Brooks & Endler 2001). This definition implies that a choosier individual is going to devote more resources to sampling among mates, and is therefore going to base mate choice off a more accurate estimate of courter trait distributions (Janetos 1980; chapter 6). However, it is useful to decouple choosiness from mate sampling, since two individuals can sample the same number of mates and nevertheless differ in choosiness.

Reinhold and Schielzeth (2015) define choosiness as “change of mating propensity with changes in trait values” and provide an extensive discussion of the underlying statistical issues. Put simply, we can quantify choosiness by measuring how concentrated chooser responses are in particular areas of trait space. For unimodal, Gaussian preference functions, choosiness can be quantified as the standard deviation of response about the peak preference (Gray & Cade 1999; fig. 1.4e); more generally, unimodal choosiness is the maximum slope of the cumulative distribution function (Reinhold & Schielzeth 2015). For directional preference functions, choosiness is expressed as the maximum slope of the linear preference function (Pomiankowski 1987; fig. 1.4f) or, for saturating functions, as the slope of the logistic regression (Reinhold & Schielzeth 2015). Models of preference evolution tend to focus on choosiness for directional preference functions and on peak preference for unimodal functions, and to ignore more complex preference functions altogether (chapter 14).

Responsiveness and choosiness are intertwined. At low levels of responsiveness—for example when an individual is physiologically unreceptive—all mates will be rejected. Similarly, at high levels of responsiveness, choosers may mate with any available mate. Choosiness in both of these cases will therefore be zero, but the consequences will be maximally different: an unresponsive chooser mates with nobody, thereby increasing sexual selection by eliminating a chooser from the mating pool. A hyper-responsive chooser mates with anybody, weakening sexual selection and promoting interspecific hybridization. Further, choosiness is where we perhaps see the biggest disconnect between measured preference functions and realized choices. This is because two choosers may be equally selective, but may differ in their observed choosiness because they encounter a different distribution of courter traits from which to make choices. I will return to the relationship between choosiness, responsiveness, and the effective distribution of courter signals (Edward 2015) in chapter 6.

### 1.6.6 A concordance of preference-function properties and behavioral mechanisms

It is useful to think about how these rather abstract properties of preference functions map on to actual behavioral mechanisms in choosers (table 1.1), since it is these mechanisms that evolve and modulate social and environmental effects on preferences. As noted above, preference involves appetitive or proceptive behaviors toward a sexual stimulus, while antipathy involves

Table 1.1. Properties of preference functions and their corresponding behavioral mechanisms

<i>Functional property</i>	<i>Behavioral mechanisms</i>
Preference	Appetitive behavior Proceptive behavior
Antipathy	Aversive behavior
Peak preference	Sensory tuning Perceptual tuning
Valence	Hedonic assignment
Responsiveness	Sensory tuning Perceptual tuning Motivation Receptivity
Choosiness	Sensory tuning Perceptual tuning Motivation Receptivity Mate sampling Comparative evaluation

aversive behavior (chapter 2). Peak preference is often a function of the tuning of the sensory periphery (chapter 3) or of downstream perceptual mechanisms (chapter 4). Valence depends on the hedonic assignment of subjective value to stimuli (chapter 5), and responsiveness depends on physiological receptivity and motivation to mate (chapter 6). Choosiness is more complicated, since it is intertwined with responsiveness as noted above, and is additionally dependent on mate sampling and mechanisms for comparative evaluation (chapter 6), and with the breadth of sensory or perceptual tuning.

### 1.6.7 Real preference functions are highly dimensional

Even the simplest preference is a so-called function-valued trait (Stinchcombe & Kirkpatrick 2012; McGuigan et al. 2008b; Rodriguez et al. 2013) where the chooser's phenotype depends on the value of a stimulus. Preferences are, however, highly multidimensional, with choosers attending to multiple interacting traits, which means that we are invariably measuring a subset of the multivariate space within which preferences operate (chapter 4).

These multivariate preference functions acquire even more dimensions when we consider that they are not hard-wired properties of individuals.

Mate-choice mechanisms can be modulated in a host of ways, starting with their sensory underpinnings (chapter 3); for example, the retinal pigments of brown trout (*Salmo trutta*) change according to season (Muntz & Mouat 1984), and the ears of female cricket frogs (*Acris crepitans*) are tuned to lower frequencies with increasing age (Keddy-Hector et al. 1992). The signaling environment changes the conspicuousness of signals and therefore their assessment by choosers (chapter 3), and choosers vary in their motivation to mate and therefore their choosiness (chapter 6). Even when tested on the same sets of stimuli under identical conditions, choosers are often highly inconsistent in their responses (chapter 9). Preferences vary according to a host of ecological factors including nutritional condition, predation risk, and parasite infection (chapter 11), and as a function of social interactions (chapter 12). All of these factors can modulate, eliminate, or even reverse preferences. If we want to characterize an individual's "preference phenotype," we need to take into account how preferences vary according to history and circumstance.

Further, preferences are heavily dependent on the set of traits being compared and on how choosers are comparing them. Chooser responses to a series of traits presented in isolation may be very different from those to a series of traits encountered by comparing among courters. Interactions among multiple traits within the same courter can have unpredictable effects on preference functions for individual traits, and the multivariate distribution of courter traits is frequently misaligned with that for preferences. I will return to each of these issues over the course of this book.

## 1.7 STAGES OF MATE CHOICE

Mate choice is not a discrete event, but rather a process with multiple, distinct stages starting well before mating and, in systems with parental care, continuing throughout the lifetime of the chooser. The importance of each of these stages varies with the natural history of the organism in question. Each stage typically involves different processes of sensation, perception, and evaluation, different mechanisms for exercising choice, and different risks and rewards for choosers and courters. It is important to note that these stages encompass social mating and thereby do not require any attempt to produce offspring; choosers can behave differently toward courters or courters' offspring depending on their sexual relationship, with consequences for fitness (chapter 8).

Mate choice doesn't even require two individuals to meet. For example, male collembolans *Orchesella cincta* deposit spermatophores. Females can

pick up only one spermatophore, and the spermatophores of males exposed to rivals are more attractive (Zizzari et al. 2013). Choosers are therefore making a decision based entirely on the “extended phenotype” (Dawkins 1983) of courters.

The convention traditionally has been to divide mate choice into “pre-mating” and “postmating” stages. Before mating, choosers behave differently toward different courters as a function of the latter’s signals and cues. After mating, choosers can exert mate choice by skewing fertilization in favor of some courters more than others, and/or by differentially allocating resources to the offspring of attractive versus unattractive courters.

The pre/postmating dichotomy is perhaps insufficient, because it fails to capture important mate-choice processes surrounding mating itself. There is also a big difference between choosers merely evaluating signals produced by courters and choosers engaging in intimate activity. Even before copulation or gamete release, physical contact increases the likelihood of pathogen transmission or physical injury. Individuals perform courtship behavior around and during mating, and fertilization bias and subsequent investment can be influenced by these behaviors (Eberhard 1996; chapter 7). It is also the case that our understanding of mate-choice mechanisms overwhelmingly comes from work on the earlier stages of choice: it is much easier to study the pre-contact stages of mate choice, for example through experimental manipulation and playback of signals, than intimate interactions where touch and contact chemical cues might be involved. I suggest that a third category, the “peri-mating” stage of choice, is useful in distinguishing interactions before and after intimate contact.

### 1.7.1 Premating

**Premating** choice involves the detection and evaluation of courter signals, and is by far the best-understood stage of mate choice. Premating choice can be performed at minimal cost to the chooser (chapter 6), and can be readily performed by both males and females. An **advertisement** (e.g., nest decorations, long-range visual displays, frog calls, or birdsong) can be generated by the courter without attending to a specific chooser, and the chooser can evaluate it without directly interacting with the courter.

In part because advertisements can be manipulated or synthesized (chapter 2), experimental studies of mate choice have overwhelmingly focused on premating processes. And because nearly all mechanistic studies have been on sensory reception, we have a rich picture of how choosers detect advertisements, and how variation in detection affects mate choice.

Detection of advertisements—distinguishing them from background noise—is obviously required for mate choice. In order for a courter to be a candidate for mate choice, a chooser has to know that it exists. Some workers see detection as a separate process from mate choice. Parker (1983) makes a distinction between “passive attraction” and “active mate choice.” In the former, choosers are simply attending to the courtiers who provide the greatest stimulation, and thereby the greatest probability of being detected. In the latter, they are discriminating among readily detected mates. This distinction is not very valuable, because the properties of “passive attraction”—for example, sensitivity to particular wavelengths of light, acoustic frequencies, or volatile molecules—can evolve and be modulated by experience and environmental input just like “active choice” can.

On the other hand, some scholars vastly overestimate the importance of detection, equating detectability to preference and preference to choice (chapter 3). As I will argue in chapter 7, much of the unexplained variation in mating outcomes relative to mating preferences lies in the later stages of mate choice. These stages are intimate and interactive and therefore more resistant to experimental study (but see chapter 7), but may in fact account for most of the variation in realized mate choice. Detection is just the necessary first step in choosing a mate, and should not be considered in isolation from the rest of the process.

Having detected a courter’s signal, the chooser then evaluates the courter. Based on that evaluation, she may respond by behaving in a way that facilitates or inhibits subsequent stages. For example, male satin bowerbirds and their kin are noted for producing elaborate courtship structures (bowers; fig. 1.1). Females evaluate the bowers first with males absent, then return to a subset of these bowers to observe courtship displays when males are on the nest. Finally, females return a third time to copulate with a fortunate minority of males (Coleman et al. 2004). In general, mate choice proceeds through increasingly close-range and individually directed phases of courtship, and blurs into the peri-mating phase.

### 1.7.2 Peri-mating

**Peri-mating** choice includes activities soon before, during, and soon after mating when partners are in close physical contact. I use “peri-mating” (Fedina & Lewis 2008) rather than the more common “pericopulatory” (e.g., South & Lewis 2012), since the former encompasses external fertilizers that do not copulate, like broadcast-spawning fishes and flowering plants. In these species, but even more so in species with internal fertilization, mating

is physically intimate and presents choosers with potential risks ranging from injury to transmission of sexually transmitted diseases. The opportunity for peri-mating (and postmating) choice is heavily skewed toward the sex with control over fertilization and provisioning, usually the female (but see, e.g., Paczolt & Jones 2010). There are ample opportunities for choosers to express preferences immediately before, during, and after mating, notably by permitting, denying, prolonging, or terminating copulation, or by physically attacking and even consuming courters (chapter 7). Just as detection has been labeled “passive choice” (Parker 1983), some workers have described peri-mating behavior as distinct from mate choice, in the context of courters “priming” choosers for mating by inducing physiological receptivity (e.g., von Schilcher 1976; Riede 1983). While courters can certainly manipulate choosers into mating, receptivity constitutes an important mate-choice mechanism, since different stimuli are better or worse at inducing receptivity (Eberhard 1996).

### 1.7.3 Postmating

**Postmating** choice is the subject of a large body of correlational and experimental work (chapter 7). Choosers can make sexual decisions after mating; first, through differentially biasing fertilization success, and second, through the resources that are invested into offspring after fertilization; a chooser behaves differently toward its offspring from different courters. The post-mating phase gives a chooser ultimate control over a courter’s fate. At the one extreme, she can devote all of her **residual reproductive value** to a single mating with a single courter, allowing only his sperm to fertilize her eggs and devoting herself to caring for their offspring at the expense of any future broods. At the other, she can kill him and eschew his sperm (Andrade & Kasumovic 2005).

## 1.8 MATE CHOICE AS A PROBLEM IN ANIMAL COMMUNICATION

Mate choice is about communication: a receiver, the chooser, must interpret a signal from the courter (Ryan 1990). This is true whether we are referring to a female fruit fly flying away from the song of a male, to hormone receptor proteins in the reproductive tract binding to signal molecules in the seminal fluid, or to the awkward give-and-take of first-date conversation. This

can be a highly dynamic process, where chooser behavior is likely to influence subsequent actions by the courter. All mate choice involves the sensation, perception, and evaluation of courter signals, and their integration into a behavioral decision. The first part of this book details how these steps operate.

**Sensation** is by far the best understood step in how choosers interpret signals, and is the focus of chapter 3. Sensation involves the conversion of stimuli in the environment into internal neural and chemical responses. Sensation is a *sine qua non* in mate choice. If a stimulus can't be sensed by a chooser, there is no way that it can influence her preference. Mechanistic studies of mate choice have overwhelmingly focused on the relationship between the **sensory periphery** (the structures like eardrums, olfactory epithelia, and photoreceptor arrays that transduce environmental information into internal information) and **detectability** (the probability of detecting a courter signal against background noise). A sexual stimulus is identified as such from a much broader pool of stimuli in a noisy environment; before it can have an effect on mate choice, it must be discernible from the background noise. As detailed in chapter 3, there has been a great deal of work on mate choice in the context of how sensory mechanisms respond to courter signals, and how this response depends on the sensory environment.

In some microbial systems, sensation is the sole determinant of mate choice; mating can only occur between individuals emitting a highly specific agonist and individuals expressing a highly specific odorant receptor. This is the case in the unicellular fungus *Cryptococcus neoformans*, where individuals respond only to pheromones from their own molecular "mating type," and both the pheromone and the response are associated with genetic variation at a single mating-type locus (Lin 2009, 2010; fig. 1.5). It should be noted, however, that even this most elementary molecular response is context-dependent (chapter 11), with factors like light and nutrient abundance modulating reproductive decisions (Lin 2009, 2010). Even in *Cryptococcus*, mate choice involves the integration of information across multiple sensory inputs.

In most animals, however, mate choice involves **perception**, whereby multiple sensory inputs, often from multiple sensory **modalities**, are integrated into a neural representation that a chooser can then use to make decisions (Levine 2000). We know that choosers attend to numerous traits during mate choice (Partan & Marler 2005; Candolin 2003), but there has been relatively little mechanistic work on how perceptual integration influences mating decisions (but see Griffith & Ejima 2009). This topic is explored in chapter 4.

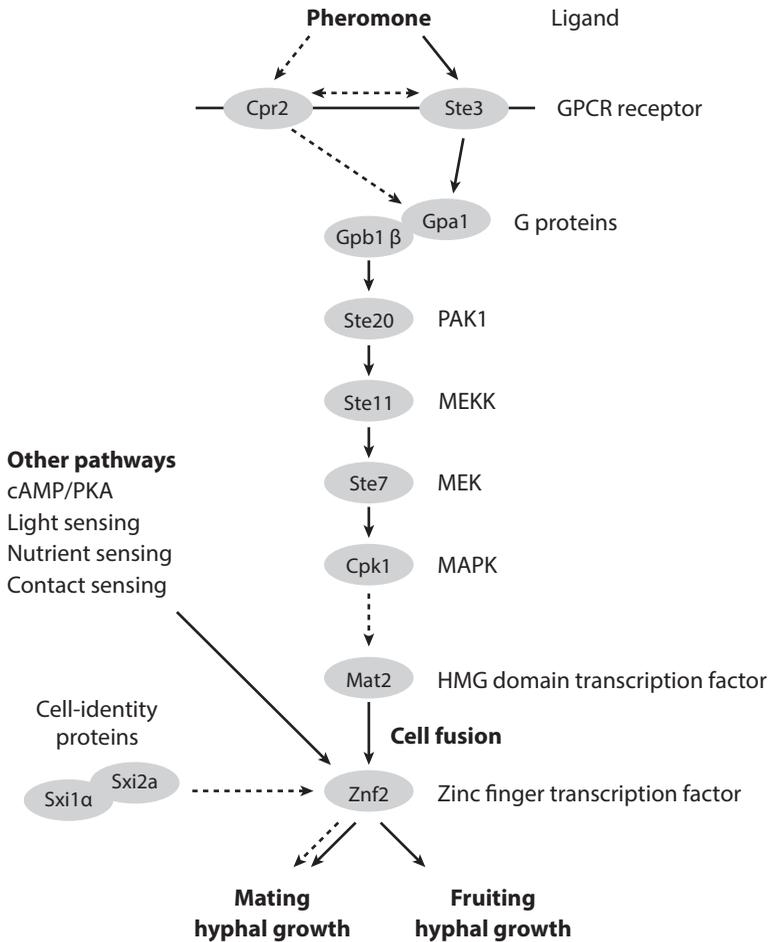


Figure 1.5. Signal transduction pathway leading to mating in the unicellular yeast *Cryptococcus neoformans*. Chemoreceptors respond to exogenous pheromones that signal “mating type,” triggering a signaling cascade that leads to cell fusion and meiosis. Environmental variables can modulate the expression of transcription factors leading to mating. After Lin (2009); Lin et al. (2010).

Perceptual representations of courtiers, or of particular features of courtiers, are assigned a valence, a positive or negative assignment of subjective value. This evaluation (chapter 5; Musch & Klauer 2003) depends heavily on the courtier’s motivational state and on the pool of potential mates (chapter 6). Evaluation, like sensation, is by definition part of mate choice. In *Cryptococcus*, evaluation is performed by the activity of the transcription

factor TF2, which integrates input from a pheromone signal with information about the environment to produce a decision whether or not to exchange genes (fig. 1.5).

Evaluation may be highly variable even among individuals with evolutionarily conserved sensory and perceptual mechanisms, as in members of the two sexes within one species. In a similar vein, the same trait is often attractive to choosers in one species and repulsive to choosers in a closely related species. For example, green swordtail females show a preference for males with a colorful “sword” ornament on the caudal fin (Basolo 1990a), while sheepshead swordtails show antipathy for the same trait (Wong & Rosenthal 2006). The traits are sensed and perceived by females in both species, but evaluated differently. Therefore, the same stimulus induces choosers to mate in some cases and to reject in others. Evaluation is discussed in chapter 5.

## 1.9 PROSPECTUS

The first section of this book describes the natural history of mating preferences and mate choice. In chapter 2, I provide an overview of how empiricists measure mate choice. Chapter 3 focuses on the importance of sensation and sensory modality in shaping mate choice, drawing on the substantial literature on the sensory ecology of mate choice. Chapter 4 discusses behavioral and evolutionary-genetic studies of chooser preferences for multiple courter traits in the light of the psychological literature on multimodal and multitrait perception. Similarly, chapter 5 uses the scant behavioral data on evaluative processes and mate choice as a point of departure to discuss the general neural mechanisms that are likely to be involved in the process of assigning subjective value to mates. Chapter 6 addresses the cognitive and ecological constraints on how choosers sample and decide among multiple candidates; chapter 7 discusses mechanisms of mate choice once mating has occurred, and chapter 8 discusses the dynamics of systems where social and/or reproductive mate choice is mutual.

The middle of the book focuses on variation in mate choice and mating preferences. Mate choice is primarily interesting because it operates so differently among species, among individuals, and even within individuals. Chapter 9 provides an overview of variation in mating preferences, focusing on the repeatability of mate choice. Chapter 10 covers genetic variation in preference, along with a brief overview of genomic approaches to elucidating the genetic basis of mate choice. Chapter 11 addresses how preferences

are shaped by the physical environment and the ecological community, including predators, parasites, and nutrition. Finally, chapter 12 considers the role of the social environment in shaping preferences, from parental effects during early development through mate-choice copying during an interaction with a courter.

The final portion of the book concerns origin, evolution, and consequences of mate choice. In chapter 13, I describe how mating preferences can arise in a context unrelated to mating, due to selection in another context or due to basic constraints on organismal function. Chapter 14 focuses on how natural selection can act directly on mating preferences as a result of costs or benefits of choosers mating with particular courters. In chapter 15, I address the core focus of contemporary mate-choice research, namely the theoretical and empirical literature concerning the co-evolution of chooser preferences and courter traits. Chapter 16 reviews the ample literature on mate choice and speciation, as well as the more novel topic of mate choice and genetic exchange among species. Chapter 17 specifically deals with mate choice and human evolution. Human examples are cited throughout the book, but the distinct corpus on mate choice from evolutionary psychology, and some of the peculiarities of what we find attractive, both require special treatment. Finally, chapter 18 concludes the book with suggestions toward a synthetic theory of mate choice.

## 1.10 ADDITIONAL READING

- Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Bateson, P. (ed.) 1983. *Mate Choice*. Cambridge: Cambridge University Press.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.
- Milam, E. L. 2010. *Looking for a Few Good Males: Female Choice in Evolutionary Biology*, Baltimore, MD: Johns Hopkins University Press.