



REVIEW

Alternative mechanisms of nonindependent mate choice

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Aspects of the environment, including the social environment, can contribute to intrapopulation variation in mating preferences. One example of the effect of social environment on mate preferences is mate choice copying; however, other types of socially influenced (nonindependent) choice might exist. We develop a list of such alternatives based on possible physiological or psychological mechanisms, evaluate the evidence distinguishing one from another and clarify some controversial aspects of mate choice copying. This framework reveals many ways in which one female's mate choice can influence that of another, and suggests a broader array of hypotheses about the selective forces acting on such mechanisms. Because nonindependent choice can occur in a variety of ways, it could be more important for understanding patterns of mate choice than current theory suggests.

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Mate preferences, typically by females for males with particular traits, are widely documented (Andersson 1994). How females gain information about potential mates and what benefits they receive from choosing particular males as mates remain unresolved issues, despite a wide array of hypotheses (e.g. Kirkpatrick & Ryan 1991) and considerable empirical study (e.g. Andersson 1994). Because such preferences can have major effects on the patterns of selection (e.g. Arnold 1983), the process of evolution, and even speciation (e.g. West-Eberhard 1983), understanding ecological and evolutionary forces that affect preferences continues to be critical for explaining the diversity of organismal traits.

Mate preferences can be variable between and within populations (Andersson 1994; Jennions & Petrie 1997). Explanations for this variation usually assume that preferences remain fixed throughout the lifetime of the organism and result from strong genetic influences (e.g. Kirkpatrick & Ryan 1991). Recent reviews, however, have highlighted evidence of substantial flexibility in mate preferences (Jennions & Petrie 1997), and increasing attention is being given to social influences on mate choice (or nonindependent mate choice: e.g. Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin 1996a; Ryan

1997). Indeed, results from some empirical studies and models suggest that nonindependent mate choice can be an important source of variability in mating patterns, causing a decrease (Gibson et al. 1991) or increase (Wade & Pruett-Jones 1990; Kirkpatrick & Dugatkin 1994) in the strength of sexual selection on male traits. Different mechanisms of nonindependent choice could have different consequences for sexual selection. Alternative mechanisms may be prevalent in nature and worthy of empirical study, but have been largely unexplored.

Studies of nonindependent mate choice have focused nearly exclusively on mate choice copying, in which mate choice of a particular male by one female causes an increased preference for that same male in another female (Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin 1992, 1996a; Brooks 1998). The study of this phenomenon has been controversial. Disagreement exists over which types of cues suitably reflect a female's mate-choice decision (e.g. Pruett-Jones 1992; Jamieson 1995; Dugatkin 1996a; Kraak 1996) and whether some benefits (e.g. increased egg survival) of choosing the same male as another female preclude copying (Jamieson 1995; Kraak 1996; Brooks 1998). Experimental designs used to demonstrate copying differ (e.g. Dugatkin 1992; Grant & Green 1996; Lafleur et al. 1997; Galef & White 1998), possibly producing differences in social effects on preferences where none exists. Such experiments have also ignored other ways females might influence the choices of other females.

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Perhaps some confusion stems from the lack of any systematic presentation of alternative ways in which nonindependent mate choice can occur. For example, suppose that a copulation event between a female and a male increases the probability that an observing female also copulates with that same male. At least two very different mechanisms could produce this result. Copying, which is considered to involve learning, could be one such mechanism (e.g. Goldschmidt et al. 1993; Dugatkin 1996a; Grant & Green 1996; Schlupp & Ryan 1997; Galef & White 1998). Alternatively, the sight of copulation could temporarily increase the female's sexual receptivity to all males. If she happened to remain close to the previously chosen male, she would be more likely to mate with that male. Although the outcome is that one female's choice is the same as another's, this mechanism does not involve learning.

Possibilities like the one described above led us to consider alternative mechanisms for nonindependent choice. Our organization of these mechanisms is similar to that for social learning proposed by Galef (1988), Heyes (1994) and Zentall (1996). By explicitly defining alternative mechanisms, that which constitutes nonindependent choice is made clearer, a set of related phenomena are made more distinct and appropriate tests for these alternatives become more obvious. Moreover, the process of considering alternative mechanisms also stimulates a broad array of new questions about the functional consequences and evolutionary impact of nonindependent choice.

Definitions

Nonindependent mate choice (Pruett-Jones 1992) occurs when the mate choice decision of one female (the 'model' female) influences that of another female (the 'focal' female). Nonindependent choice is a form of plasticity in choice behaviour; interactions between a male and another female provide information that alters the focal female's subsequent mate choice behaviour.

A mating interaction between a male and the model female could alter a male trait (e.g. increase display rate) that females normally prefer, thereby altering the probability that the focal female will choose that male. Pruett-Jones (1992) did not consider this to be nonindependent mate choice. This restriction focuses attention on how females respond directly to the choice behaviour of other females. Nonindependent choice and mate choice copying could be mistaken as the same thing. We do not restrict the definition of nonindependent choice in the same way, and we will present arguments that copying is only a minor subset of the possible types of nonindependent choice. Indeed, in our view, a clearer definition of copying emerges from taking a broad approach to nonindependent mate choice.

We also agree with Kraak (1996) that mechanisms should be defined irrespective of whether they have adaptive value. Alternative mechanisms by which nonindependent choice occurs could evolve for a variety of reasons. Yet, Jamieson (1995) and Brooks (1998) both included aspects of function in their definitions of

copying. Jamieson (1995), for example, contended that, in fish, female choice of males with eggs is not 'copying' if the presence of eggs increases the probability that the focal female's eggs survive. We maintain that including possible adaptive functions of a phenomenon into an operational definition confounds the criteria for demonstrating the phenomenon and explanations for how it might have evolved (i.e. mixing levels of analysis: Sherman 1988). Although distinguishing features of possible mechanisms are not based on fitness consequences in our framework, we will return to functional issues later in order to evaluate the evolutionary stability of the proposed mechanisms.

Mechanisms that Produce Mating Patterns Suggestive of Nonindependent Choice

Nonindependent mate choice should give rise to nonrandom mating patterns, but so can other processes. Nonrandom mating can result from either independent or nonindependent mate-choice decisions. Because documenting such mating patterns is often an initial step for investigating nonindependent choice (e.g. Wiley 1973; Gibson et al. 1991), we first point out ways such patterns can arise that give the false appearance of nonindependent choice.

Kin-associated genetic preferences

In a variety of animals, female kin remain associated throughout their lives (e.g. some cooperatively breeding birds: Brown 1987). If so, and if variation in female preferences has a strong genetic component, then common genetic influences could produce more similar preferences among social associates than among females selected randomly from the population.

Common environmental effects

Common environmental effects on individuals of a group, with subsequent association among them, could cause the mate choices of social associates to be similar. For example, the level of nutrition in a particular area might affect the dominating ability or movement patterns of several females, and thus influence similarly the types of males each female encounters.

Consexual attraction or repulsion (consexual cueing)

Several authors (e.g. Pruett-Jones 1992; Clutton-Brock & McComb 1993; McComb & Clutton-Brock 1994; Dugatkin 1996a; White & Galef 1999a) have noted that grouping by females could result in nonrandom mating patterns without an influence of one female's mate choice on that of another. Because a given group of females might encounter the same subset of males, individual females within groups will be more likely to mate with the same male. A clear example of this occurs in fallow deer, *Dama dama*, in which female decisions to associate with a male are best explained as preferences for being in a larger group (McComb & Clutton-Brock 1994).

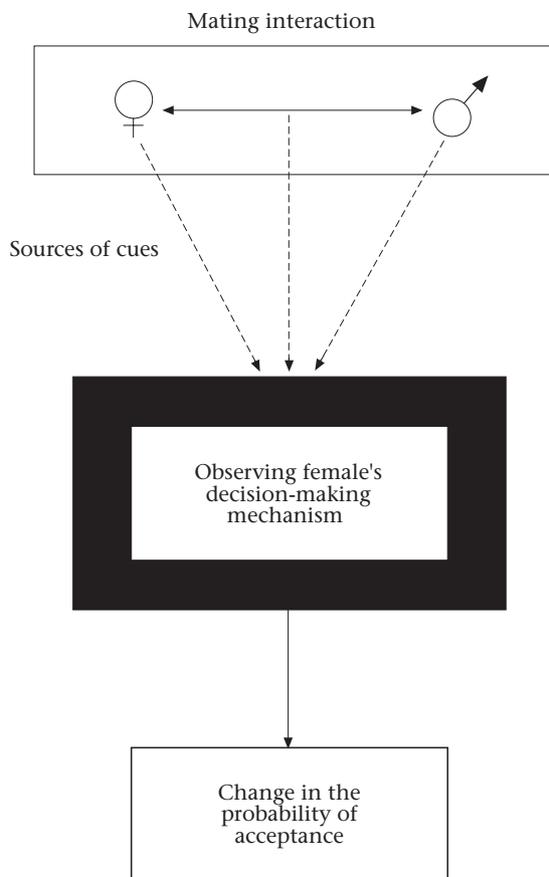


Figure 1. A general model of nonindependent choice (sensu Sherman et al. 1997). A mating interaction between a male and a female produces cues (via male, model female, or both), that are perceived by the focal female, resulting in a change in the probability she accepts a particular male as a mate. Mechanisms differ in how a cue produces a change in that probability.

Interactions between conspecifics could produce overdispersion as well. Overdispersion could indicate non-independent choice, or could merely result from females avoiding other females. For example, female territoriality prior to mate choice, such as that of the dunnock, *Prunella modularis*, in early territory establishment (Davies 1992), causes overdispersion but not nonindependent choice.

NONINDEPENDENT MATE CHOICE

All mate choice is a problem of recognition (Sherman et al. 1997); typically, males produce signals (production), females compare them to some criteria (perception) and then decide whether to copulate (action). Non-independent choice complicates this process, because some cue of another female's mate choice decision affects the perception and/or action components of the focal female's decision making. In this paper, we focus on the alternative mechanisms connecting cue with response (Fig. 1). Cues of a previous mate choice decision arise from an interaction between a male and a female, and so could come from the model female, the male, or some

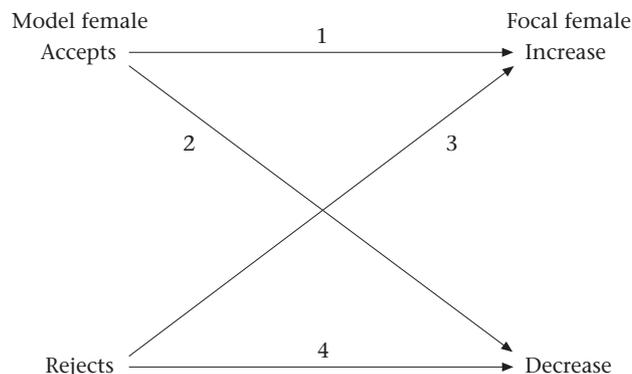


Figure 2. The four types of influence of one female's mate choice on another's. The right column indicates the change in probability that the focal female makes a particular mate choice. Each of these four types of influences may be possible for each of our proposed mechanisms.

combination of the two (Kraak 1996). A cue, therefore, is anything that provides information about a model female's mate choice decision, and so could be produced before or after her choice. The information provided by those cues could be processed in a variety of ways. We focus on two major groups of mechanisms: those that do not require learning and those that require either associative learning, or cognition.

For each mechanism, four types of influence could link the choice made by the model female with the behaviour of the focal female (Fig. 2). The model female could either reject or accept the male involved. This could result in either an increase or decrease in the probability the focal female chooses to mate with a particular male (Pruett-Jones 1992). In theory, each of the possible mechanisms we discuss below could produce any of these four types, although some combinations of mechanism, cue and type of influence seem unlikely. We do provide examples of some relationships that have received little attention (Table 1), such as avoidance of previously mated males, but that are likely to be quite common in some cases (e.g. in monogamous birds or spermatophore-limited insects and amphibians).

Nonlearned Responses

Stimulus enhancement/reduction

Mating often consists of conspicuous displays and pre- and postcopulatory behaviour (e.g. Hasson 1991). Copulation itself is often conspicuous (e.g. via thrusting, wing flapping or loud vocalizations: Clutton-Brock et al. 1982; Birkhead & Møller 1992). Such conspicuousness could attract the attention of the observing female. Attracting a female's attention is likely to lead to a higher probability that the mating male will be included in the set of males the focal female evaluates. As a result, females are more likely to choose mating males, simply because those males are more likely to be noticed, thereby producing nonindependent mate choice.

We note that the term 'stimulus enhancement' has been used to denote a type of social learning (e.g. Galef

Table 1. A selection of real or potential examples of each alternative mechanism of nonindependent choice*

Mechanism	Change in probability that focal female makes a particular mate choice	
	Increase	Decrease
Nonlearned		
Stimulus enhancement/reduction	Presence of female near male makes him more likely to be detected (and therefore assessed) than lone males	Pairs go into hiding to copulate; copulating males are therefore less likely to be noticed than males not copulating
Contagion/inhibition	Male postcopulatory display increases female receptivity to all males	In a dominance hierarchy, mating by the alpha female induces reproductive suppression in subordinates
Stimulus response	Females prefer males with eggs to those without (fathead minnow, <i>Pimephales promelas</i> : Unger & Sargent 1988)	Paired males advertise less (burying beetle, <i>Necrophorus defodiens</i> , in which female attacks her mate if he advertises: Eggert & Sakaluk 1995)
Learned		
Association-to-location	Females copulate at sites where they earlier observed high display rates, which are correlated with copulation success (some lekking birds: Gibson et al. 1991)	Female avoids copulating at sites where she previously saw a male–female pair (pied flycatcher, <i>Ficedula hypoleuca</i> : Alatalo et al. 1981)
Association-to-male	Observing female prefers male previously seen near a female over a male that appeared to be alone (Japanese medaka, <i>Oryzias latipes</i> : Grant & Green 1996)	Cue that model female resisted a copulation leads focal female to avoid that male in a later encounter
Association-to-trait	After observing the mate choices of older females, inexperienced females prefer similar males	Female prefers males that do not resemble her father (the male chosen by her mother) and consequently avoids inbreeding depression (Japanese quail, <i>Coturnix japonica</i> : Bateson 1982)
Cognition	Observing female adopts a form of idiosyncratic courtship that was used successfully by the model female	After observing a male compromise his offsprings' survival, females avoid mating with that male in order to avoid a similar outcome

*Not all types of influence (Fig. 2) or sources of cues are depicted.

1988; Heyes 1994) in which the behaviour of the model draws attention to a stimulus that then is involved in single-stimulus learning, such as sensitization or habituation. Because the perceptual enhancement of a stimulus by a model can affect other, nonlearned behaviour, the concept of stimulus enhancement should not be confined to just learned behaviour. Our use of the term here emphasizes the perceptual effects on a case of nonlearned behaviour.

Most experiments on nonindependent mate choice have not explicitly tested for stimulus enhancement. Nevertheless, stimulus enhancement is probably eliminated by using an experimental design that facilitates the evaluation of both males (in binary choice tests) by the focal female. Typically, after the observation phase (when the focal female observes two males, one of which is interacting with the model female) and before the test phase (when the focal female's preferences for previously observed males are tested, e.g. Dugatkin 1992; Galef & White 1998; Brooks 1999), experimenters swap the locations of the two males

and remove the model female. This design prevents stimulus enhancement from occurring during the test phase. It does not test for the presence of stimulus enhancement, so the prevalence of this mechanism is unknown.

Acceptance by the model female leading to an increased probability that the focal female chooses the same male seems to be the most likely type of influence via this mechanism. However, rejection behaviour is also conspicuous in some species (e.g. female resistance of attempted forced copulation in waterfowl: McKinney et al. 1983). Conspicuousness of any sort makes a male more likely to be noticed by a female, and so we would predict that if stimulus enhancement alone were operating, conspicuous rejection would also lead to an increased likelihood of a male being chosen as a mate.

Stimulus reduction occurs when a mating causes a male to become less conspicuous to other females. For example, mating could attract predators. If, in response to that risk, copulation occurs in hiding, then a chosen male may also be inconspicuous to conspecifics. This male will

be less likely to be assessed by other females, and hence less likely to be chosen by them.

Altered general receptivity (contagion/inhibition)

Early ethological reports on colonial species, particularly in birds, document waves of copulation between pairs (Darling 1938; Brown & Baird 1965). Copulation in one pair is apparently a stimulatory cue for copulation of other pairs. Presumably this behaviour is common when synchronous breeding is beneficial. An unpaired female might experience a similar effect. If she and the male stay in the same location for a time, then this behaviour could lead the focal female to copulate with the same male as the model female. We call this effect 'contagion', which occurs when the cue of another female's mate choice leads to an increase in the focal female's sexual receptivity to all males.

Inhibition occurs when the cue of another female's mate choice decreases the focal female's general sexual receptivity. For example, copulation by a dominant female could suppress receptivity in subordinates, and reduce their probability of mating with the same male.

Altered general receptivity is distinct from stimulus enhancement because it alters female sexual receptivity to all males encountered, whereas stimulus enhancement alters a female's short-term perception of which males are present. A test for this mechanism is to shift the location of the focal female or swap males; any changes in receptivity due to the cues of another female's mate choice should persist. Both male and female cues could lead to increases or decreases in general receptivity (Table 1).

Few of the previous studies of nonindependent choice have considered contagion as a potential competing mechanism, but most experiments probably eliminated it as a possibility anyway. In two-way choice arenas, contagion might produce nonindependent choice if the focal female does not have a chance, between observing the model female choosing a male and being tested for her own preference of male, to move away from the male she just witnessed copulate. However, in most such studies, delays between observation and test phases and/or moving the focal female to a central holding area briefly before the test phase (e.g. Dugatkin 1992; Dugatkin & Godin 1993; Brooks 1996; Lafleur et al. 1997; Schlupp & Ryan 1997; Galef & White 1998) reduce the likelihood that contagion explains these examples of nonindependent choice.

Nonlearned stimulus response

Nonlearned stimulus response occurs when a cue of one female's mate choice has an immediate and temporary effect on the probability the focal female chooses that same male (Table 1). In this mechanism, the focal female has an altered probability of choosing the mated male only. In contrast to contagion, the female's receptivity to other males is unchanged. In addition, learning is not involved; the effect on preference lasts only as long as the cue is present. This mechanism could occur when mating interactions magnify male traits normally used by females in assessing potential mates (e.g. Knapp &

Kovach 1991; Sargent et al. 1998). An observing female might then perceive these males as matching her criterion for an acceptable mate. If such enhanced traits were sufficiently costly for males to produce, then expression at times other than during mating interactions would not be favoured and this mechanism of stimulus response could be evolutionarily stable.

Acceptance by the model female can also decrease the probability of mating by the focal female via this mechanism. For example, in the sagebrush cricket, *Cyphoderris strepitans*, female choice is based on the size of male nuptial gifts (his wings, which the female eats during copulation). Prior matings reduce those traits, reducing the attractiveness of the male to females (e.g. Morris et al. 1989; Johnson et al. 1999). Nonlearned stimulus response also occurs when a mate-guarding female is aggressive to other females and deters them from copulating with her mate. If, in her absence, other females become receptive to that male, then stimulus response is implicated.

Several studies of mate choice copying have controlled for the possibility of nonlearned stimulus response, primarily by inserting delays between the initial observation of mate choice and testing for the effects on the focal female's decision (e.g. Dugatkin 1992; Galef & White 1998). Dugatkin (1992) ruled out this mechanism in guppies, *Poecilia reticulata*. Females that witnessed a prior choice preferred the chosen male, but naïve females did not prefer previously chosen males, indicating that those males were not merely retaining an enhanced trait from the prior mating interaction.

Nonindependent Choice via Learning

Nonindependent choice can also arise through adjustments in the rules by which females judge males, that is, adjustments linked causally to another female's mating decision. Such changes constitute a higher level of plasticity (i.e. learning) than the unlearned mechanisms described above. Most studies of nonindependent choice to date have been seeking evidence of females learning about males via watching other females. We develop several alternative ways this could occur. We emphasize again that all mechanisms, including associative learning, could be focused on cues arising from the male, the model female, or the combination of the two.

Association to a location

One possible learned response is for a female to associate some cue of a mating with a location. If male site fidelity exists, then by preferring to mate at the same location as the model female, the focal female is more likely to mate with that same male. Gibson et al. (1991) found that female sage grouse, *Centrocercus urophasianus*, return to the same territory on which they mated the previous year. They also found the mating success of males in their first season on a territory varied in relation to the mating history of the territory, rather than the male. This could be because females independently judge central territories to be better, or because females associate copulatory activity of others with the site and return

there to copulate. A distinguishing feature of this mechanism is that an association between the cue and the location is made, that then influences female mate preferences even after the cue has disappeared.

Association to a location could generate either an increase or decrease in mating probability (Table 1) in response to any cue, be it produced by the model female or the male. In some lek species, females prefer to mate at locations where earlier they witnessed especially high levels of male courtship or copulation (Höglund et al. 1990, 1995; Höglund & Alatalo 1995). Similarly, female fish with a preference for nests with eggs (e.g. Marconato & Bisazza 1986; Knapp & Sargent 1989) might inspect nests for eggs and return to spawn there. For this to be association to location, rather than stimulus response, females must prefer spawning sites that had eggs even if the eggs have been removed. However, to our knowledge this experiment has not yet been done. Finally, a female might later avoid a location where she earlier witnessed another female courting or copulating (Brooks 1999), or where she received an aggressive reaction from the model female.

Several studies of nonindependent choice have controlled for association to location by switching the locations of males between the observation and the testing stage (e.g. Dugatkin 1992; Galef & White 1998; Brooks 1999). However, the importance of association to location to free-living females may be underestimated in the laboratory. Differences in features of the location, probably an important component of association to location, have not been manipulated in experiments. By attempting merely to rule out association to location, researchers could be missing evidence of its existence.

Association to a male

Association to a male occurs when the focal female forms an association between the cue of the model female's mate choice decision and the male involved. Subsequently, the focal female's probability of mating with that male is altered, even after the cue has disappeared. For example, in Japanese medaka, *Oryzias latipes*, females prefer males which they previously witnessed spawning with another female (Grant & Green 1996). In contrast, female lemon tetras, *Hyphessobrycon pulchripinnis*, are more likely to reject males they previously observed spawning, and so avoid sperm-depleted males (Nakatsuru & Kramer 1982).

Such association to a male could occur regardless of the type of cue. Several studies have found that the observing female attends to the behaviour of the model female and associates her acceptance with the male (e.g. Schlupp et al. 1994; Grant & Green 1996; Patriquin-Meldrum & Godin 1998). Another possibility is that a mating interaction temporarily alters a male trait that is remembered by the focal female after the change has disappeared. Some authors do not consider this to be nonindependent choice (e.g. Pruett-Jones 1992). However, in this scenario, the mating behaviour of another female clearly alters the focal female's probability of mating with a particular male. In our view this mechanism qualifies

as nonindependent choice via the association-to-male mechanism.

Studies of guppies provide evidence of association to a male via male cues. Female guppies prefer males previously seen in proximity to a model female (Dugatkin 1992, 1996b; Dugatkin & Godin 1992, 1993; Briggs et al. 1996). However, the focal female shows no preference when the male, but not the focal female, is prevented from seeing the model female (Dugatkin 1992). Dugatkin tested for a residual effect of the model female on male traits (see unlearned stimulus response above) and found none. However, he did not test for the possibility that the focal female formed a preference for that male because of his behaviour (e.g. increased courtship) while viewing the model female. The focal female's memory of her preference could have produced the change in her behaviour during the test phase of the experiment. Several other studies have controlled for this (e.g. Schlupp et al. 1994; Grant & Green 1996; Patriquin-Meldrum & Godin 1998) by allowing both males in binary choice tests to see females nearby, but allowing the focal female to see only one. Results from this type of experiment in Japanese medaka indicate that both a male cue (changes in male courtship) and a female cue (the female act of spawning) altered the focal female's preference for that male even when both cues were no longer present (Grant & Green 1996).

We emphasize that rejection behaviour could also be a cue associated with the male. In addition, acceptance by the model could lead to rejection on the part of the observing female, especially in monogamous species (Table 1). One interesting example of this might occur when aggression by a paired model female is remembered by the focal female, which subsequently avoids that particular male, even in the absence of the model female.

Association to a trait

Association to a trait occurs when the focal female associates a cue arising from a model female's mate choice decision with a trait of the male and alters her sexual receptivity to any male possessing that trait. For example, consider a monogamous bird species in which male parental quality has an effect on female fitness, but which traits best signal paternal quality vary between seasons, perhaps due to environmental variation having effects on trait development. Females unfamiliar with the males in the local population (e.g. young females) might observe the traits of males that are paired, and then rank unpaired males along that trait axis. Similarly, suppose male traits are correlated in such a way that a trait expressed only during courtship to the model female covaries with one expressed all the time. A focal female might observe a male's display during courtship and learn that relationship, thereby altering her receptivity to males with the continuously expressed trait.

Kirkpatrick & Dugatkin (1994) modelled the evolution of a trait that they called copying, but which we would classify as association to a trait. Laland (1994) also presented a model of cultural inheritance, whereby a preference for a male trait is learned by social interaction with other females. Brooks (1998) defined an alternative to

copying, termed cultural inheritance, which is consistent with our description of association to a trait.

Sexual imprinting is a subset of the association-to-trait mechanism. Early experience with parents is known to influence mate preferences (e.g. [Immelmann 1972](#); [ten Cate & Bateson 1988](#); [Collins & ten Cate 1996](#)). In sexual imprinting, the parental behaviour of the male indicates the model's (the mother's) choice. An association between the trait of that male and his behaviour as a parent subsequently affects the choice behaviour of an offspring towards males other than her father. Filial imprinting (e.g. [Choudhury & Black 1994](#)) is also association to a trait, as the siblings' phenotypes depend in part on the mother's choice of mate.

Cognition

The learning mechanisms described above do not specify any cognitive processes. In this sense, they are examples of stimulus-stimulus or associative learning as described by [Heyes \(1994\)](#). That is, the mating interaction between a male and a model female exposes the focal female to a relationship between the cue of mate choice and the location, male or trait, which alters her behaviour at some future time. The psychological literature on social learning has focused on cognition, which, several argue, requires more complicated mechanisms than associative learning (e.g. [Galef 1988](#); [Heyes 1994](#); [Zentall 1996](#)). [Heyes \(1994\)](#) suggested that cognition be defined as observational learning of operant conditioning. That is, observation of a model receiving a reward for its response to a stimulus affects the behaviour of the focal individual to that same stimulus at some future point (e.g. [Akins & Zentall 1998](#)). Imitation is the special case when the observer matches the behaviour of the model, behaviour not normally displayed in the context of the task at hand. By adopting the model's behaviour, the observer appears to have a goal (obtaining the reward) in mind and understands that the model obtained that reward by use of that behaviour (e.g. [Galef 1988](#); [Heyes 1994](#); [Zentall 1996](#)), a process that is distinct from associative learning.

It is not clear whether such cognitive mechanisms apply to nonindependent mate choice. None of the patterns of nonindependent mate choice currently described in the literature would require explanations involving these mechanisms. However, such mechanisms could exist. If so, researchers might study them if they could find the correct approach.

Finding such an approach could be difficult. A key distinction between operant conditioning and the associative learning mechanisms described above is the existence of a reinforcer in the former. Distinguishing between associative learning and cognition thus requires objectively defining the difference between a stimulus, a reinforcer, and the behaviour being imitated. In the case of a model female copulating with a male, such distinctions may be difficult to make. Copulation could be a stimulus associated with a male, a reward for a type of courtship behaviour of the model female, or the target behaviour being imitated.

That said, we briefly examine what would constitute evidence of cognition as nonindependent choice.

Suppose a female courts a male that she saw provide nuptial gifts in response to another female's courtship. This could occur through either cognition or associative learning. Cognition is implicated if the focal female adopted a new form of courtship only after the model, by courting in that same way, received nuptial gifts from the male. If adoption of idiosyncratic courtship by females actually leads to higher probabilities of some males mating, then non-independent mate choice will have occurred through imitation. This mechanism could also involve male cues (such as paternal behaviour) if a female deduces rewards or punishments (e.g. the quality of care) and alters her preference for that male accordingly ([Table 1](#)). However, such examples might be difficult to distinguish empirically from associative learning mechanisms.

DISCUSSION

We have described an array of mechanisms that could result in nonindependent mate choice. These mechanisms differ in exactly how a cue to a previous mate choice decision is translated into a response; different mechanisms involve different processing of information, including unlearned responses, learning and responses involving cognition. Furthermore, the male, female, or a combination of the two involved in the prior mating can produce the cues. Finally, non-independent mate choice generates four possible types of influence linking the decision of the model female with the behaviour of the focal female ([Fig. 2](#)).

Below, we discuss several important implications of our definitions of different mechanisms for the study of nonindependent mate choice. Most of these focus on the mechanism level of analyses, even though we became interested in nonindependent choice because of questions about its function. We have found that considering alternative mechanisms generated a number of fascinating new hypotheses about the selective consequences of nonindependent choice. We will describe some of those briefly at the end of the Discussion.

Alternative mechanisms might exist in more species and contexts than previously thought. Nonindependent choice can occur through many different mechanisms and produce a variety of outcomes. Studies that have focused on demonstrating just one mechanism, so-called mate choice copying (e.g. [Dugatkin 1992](#); [Lafleur et al. 1997](#); [Schlupp & Ryan 1997](#); [Galef & White 1998](#); [Patriquin-Meldrum & Godin 1998](#)), have, for the most part, used careful control conditions that have eliminated some of the other possible explanations for the observed pattern of choices. However, such control with a narrow focus on demonstrating copying may result in overlooking the existence of other mechanisms of nonindependent choice. Balanced consideration of these alternative mechanisms and the four possible types of influences ([Fig. 2](#)) opens the door for exploring nonindependent effects in any system with nonrandom mating patterns. For example, monogamy in birds seems likely to come about by at least one of the mechanisms of non-independent choice we have described, but little attention has been given to this possibility. Mechanisms of

nonindependent mate choice by males also appear to be involved in some forms of male paternity assurance; information from previous interactions between a potential mate and another male might reduce male interest in particular females as prospective mates (e.g. White & Galef 1999b).

Another implication of our framework is that it helps clarify some confusion about the definition of and the empirical support for copying. Two potential confusions exist about the meaning of the word 'copying': (1) whether it refers to the outcome or the mechanism of mate choice; and (2) whether it results from any cue of a mate choice or just a subset. The latter contains two areas of confusion; whether copying can occur via male cues and how directly a cue reflects the model female's mate choice decision. We discuss these confusions below and offer our own definition. In the end, these confusions lead us to advocate dropping the term 'copying' entirely because of its vagueness.

Casual use of the word 'copying' could obscure potentially important and biologically distinct processes. 'Copying' could be defined broadly as occurring whenever a focal female chooses the same male as another female. As stated, however, this would include all of the mechanisms that we have discussed plus many that would be considered independent (e.g. conspecific cueing, independent preferences for the same trait, etc.). It seems clear that many authors (e.g. Pruett-Jones 1992; Dugatkin 1996a) do not consider these to be copying. These restrictions on the definition of copying focus attention on the types of cues used and through what mechanism. How, then, would 'copying' correspond to our list of mechanisms?

Dugatkin (1996a) suggested that copying requires that the focal female observe the model's behaviour (female cues in our framework). Also, he implied that it was a learned response, corresponding to our association-to-male mechanism. In Dugatkin's (1992, 1996b) empirical work on copying, he does not rule out association to a male via male cues. Other researchers have focused more tightly on association to a male via female cues; for example, Grant & Green's (1996) and Patriquin-Meldrum & Godin's (1998) experiments on Japanese medaka and sticklebacks, respectively, controlled for association to a male via male cues and demonstrated that females were using female cues.

We suggest that 'copying' best corresponds to a subset of the association-to-male mechanism, in which a female associates a cue from the model female with the accepted or rejected male, thereby increasing or decreasing, respectively, the probability that she mates with him. This definition excludes any cases of association to a male based on male-generated cues and all other learned mechanisms. Nonlearned stimulus response might be considered by some to be copying, because the focal female observes a mate choice decision and responds similarly. However, if copying were considered a learned mechanism, then this mechanism would not qualify.

Defining copying in this way has some interesting consequences. First, it emphasizes that copying may be a minor subset of the possible types of nonindependent

choice. By making the definition more rigorous, we may reduce the relative importance of 'copying' per se, but we simultaneously increase the possibilities for non-independent choice. Our definition of copying also clarifies an interesting disagreement about the types of cues involved. Pruett-Jones (1992) suggested that, in fish, female preferences for males with eggs in their nests are examples of copying. Both Jamieson (1995) and Dugatkin (1996a) disagree, based largely on functional reasons (which we maintain are not relevant to defining mechanisms). Dugatkin (1996a) and Kraak (1996) also noted that females do not actually observe the choice of other females when choosing based on the presence of eggs. Pruett-Jones (1992) stated 'it is the action, and not the consequence of the choice of one female that influences the decision of another female' and Dugatkin emphasized that females must gain information about another female's choice from direct observation. These arguments do not support the view that eggs are suitable cues for nonindependent mate choice.

We take a different view. The process of making a mating decision is a mental event that is not directly observable, so all evidence of a mate choice is a consequence, or indirect cue, of that decision. All tangible events in a mating interaction, such as copulation or laying eggs, provide information about such decisions. Eggs are therefore as suitable a cue of a mate choice decision as any other. If the decision were about with whom to entrust eggs, then eggs would seem to be a good indication of a previous female's decision. Alternatively, if the decision is about who will fertilize a female's eggs, then all cues are indirect, because fertilization cannot be directly observed, especially in internally fertilized species. Copulation itself is an indirect cue to female choice of sire, because postintromission, or 'cryptic', female choice of sires may be frequent (e.g. Eberhard 1996).

Whether a preference for males with eggs constitutes copying depends on the precise mechanism that turns the cue into a response. For example, the sight of eggs could be immediately stimulatory to a female, increasing her probability of spawning, either generally to any male nearby (contagion) or specifically to a particular male (nonlearned stimulus response). Alternatively, a female might observe eggs in a nest and subsequently remember that situation. She might associate the eggs with the nest site, and therefore display an association to a location, or she might associate eggs with the male, and therefore display an association to a male. Regardless, the cue of eggs would be involved in nonindependent choice. This example thus illustrates the importance of considering distinct alternative mechanisms leading to such nonindependence, and emphasizes the potential for confusion inherent in the word 'copying'.

A third important implication of our framework of mechanisms is that it helps develop experimental tests for particular mechanisms. We have included some evaluation of methods for testing alternatives above. Here we point out that, generally, conceptual separation of the sources of cues (male or female) to a prior mating decision leads directly to experimental designs which control for, or manipulate separately, male or female traits affected by mating interactions. Nonlearned mechanisms do not

require memory whereas learned ones do. Experimental designs that manipulate delays between observation and test phases as well as interchange males would help distinguish among those types of mechanisms.

Finally, defining distinct alternative mechanisms for nonindependent choice can lead us to consider a wider array of functional questions about nonindependent choice. To date, attention has been focused only on why copying would evolve as opposed to independent mate choice (e.g. Dugatkin 1996a). In developing our list of alternatives, we became intrigued with a host of more subtle questions. Why, for example, might a mechanism like association to a location, a male, or a trait evolve instead of contagion or a nonlearned stimulus response? All produce the outcome of a female being influenced in her mate choice decisions by the choice of the model female. How do errors in recognition (e.g. Sherman et al. 1997) vary for each mechanism? What might be the potential costs of more complicated learning mechanisms that would favour unlearned responses? Conversely, what ecological conditions would limit the effectiveness of simple mechanisms thereby selecting for more sophisticated ones? How would such mechanisms fare in evolutionary games between the sexes? If females attend to cues coming from males, then selection could favour males that display those cues all the time, not just during mating interactions. Egg theft by male fish is one potential example of falsely advertising a previous mating (e.g. Mori 1995). Selection on males to cheat could make some mechanisms, particularly those involving male cues, evolutionarily unstable, and could provide the setting for some interesting coevolutionary games between the sexes. However, many male traits are displayed only during late stages of mating interactions (e.g. courtship behaviour), despite the possibility that these traits increase the male's attractiveness to other females. Perhaps there are factors leading to opposing selective pressures that limit shifting of such cues to nonmating contexts. These issues only became apparent after we began to distinguish alternative mechanisms.

In summary, we have presented a framework for considering alternative mechanisms leading to nonindependence of mate choice. This framework provides hints that nonindependent choice may be important in more contexts than previously considered, clarifies some disagreements over definitions and experimental approaches, and stimulates a host of new functional questions about female mate choice. Our approach reveals much that we do not know about how and why nonindependent choice occurs. Our list of mechanisms will at least give new empirical studies alternatives to consider, and may provide the impetus for comparative studies that can explore some of the new mechanistic and functional questions that have emerged.

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