

The (mis)concept of species recognition

Tamra C. Mendelson¹ and Kerry L. Shaw²

¹Department of Biological Sciences, University of Maryland Baltimore County, 1000 Hilltop Circle, Baltimore, MD 21250, USA

²Department of Neurobiology & Behavior, Cornell University, Seeley G. Mudd Hall, Tower Road, Ithaca, NY 14853, USA

To many, the concept of ‘species recognition’ is integral to the origin and maintenance of species. However, the heuristic value of species recognition is hampered by its reliance on the problematic concept of species. In this paper, we first discuss assumptions associated with prevailing use of the term, including the typological implications of the concept, the false dichotomy of compatibility and mate quality, and the commonly held model of species recognition in which animals determine taxonomic status before mate status. Subsequently, we propose research directions aimed to improve our understanding of the role of courtship behavior in speciation. We propose two complementary research approaches, one addressing the processes that drive the evolution of mate recognition systems and the other addressing the phenotypic architecture of behavioral isolation. Our approach emphasizes the fitness consequences and multidimensional nature of mate choice.

Species recognition and the ‘species’ problem

As research into the origin of species comes into greater focus [1,2], clarifying the conceptual foundation of the process becomes increasingly imperative. The concept of ‘species recognition’ has long been considered a stable part of this foundation, emerging from our effort to understand the role of sexual communication in the origin and maintenance of animal diversity. Since the emergence of modern evolutionary biology [3–5], special attention has focused on differences in courtship behavior among closely related species, the importance of these differences in restricting gene flow, and consequently their role in behavioral isolation and speciation. Differences in mate recognition systems that result in behavioral isolation are commonly, although not universally, thought to evolve due to sexual selection within species and now function in the capacity of species recognition [6,7], apparently forming an ontological bridge between microevolutionary process and macroevolutionary pattern.

We argue, however, that the term ‘species recognition’ is poorly defined, and that its current usage obfuscates our understanding of the role of behavior in speciation by encouraging assumptions that are both unnecessary and misleading. Here, we examine limitations of the term ‘species’ in this context and highlight assumptions associated with the prevailing use of the term, including the typological nature of the concept, the false dichotomy of

compatibility and mate quality, and the commonly held model of species recognition in which animals determine taxonomic status before mate status. We conclude by outlining two main pathways by which diverging lineages become behaviorally isolated and then direct our attention to the phenotypes involved. We suggest that a shift in our approach to this subject, away from the conceptual framework of ‘species’ toward one based on fitness consequences and evolving phenotypes, would dramatically improve our prospects for understanding the role of communication in animal speciation.

What is species recognition?

Despite many papers addressing the topic in some form, an explicit definition of species recognition is difficult to pinpoint in any major text or influential publication. Andersson [8] considers species recognition to be a subset of mate recognition. Ryan and Rand [6] define mate recognition “...as a behavioral response indicating that one individual considers another an appropriate mate, even if mistakenly,” but fail to define species recognition.

The question of whether and why animals most often mate with conspecifics requires rigorous scientific investigation based on clear, operational definitions. If we were to attempt to define species recognition by borrowing from definitions of individual recognition [9] and kin recognition [10], species recognition might be stated to be “a measurable difference in behavioral response toward conspecifics as compared to heterospecifics”. However, we suggest that a constructive definition of species recognition should be free of associated hypotheses or mechanisms to explain it, and for that reason, even the simplified definition above imposes both conceptual and practical limitations, due to the problematic and relative term ‘species’.

The ‘species problem’

On a conceptual level, our difficulty in finding a working definition of species recognition is perhaps not surprising, because that first would require identifying a working definition of species [11,12]. In practice, the task of naming

Glossary

Compatible mate: a mate with whom a focal organism can produce viable, fertile offspring.

Mate quality: the effect of a mate on the direct and indirect fitness of its partner.

Necessary mate recognition signals: sexual signals that are a necessary prerequisite for attracting a compatible mate.

Corresponding author: Mendelson, T.C. (tamram@umbc.edu).

species – hypothesizing boundaries between taxa that might continue to share trait variation – has challenged taxonomists since before Darwin. Theoretical treatments of the species problem are no less controversial, resulting in dozens of species concepts and no universal consensus on the nature of ‘species’ [11], probably due to the varied means by which species differentiate [13]. Because all species designations are model-based hypotheses in practice, the term ‘species recognition’ can never be hypothesis-free, and will forever beg the question: what exactly do organisms ‘recognize’ when they express ‘species recognition’?

On a more practical level, the expression of species recognition almost certainly depends on the identity of the referenced heterospecific. Species recognition exhibited by a focal organism in the face of one heterospecific might disappear when presented with another, more closely related species, or one of more similar phenotype. Thus, species recognition under any definition would be operational only when the heterospecific from which conspecifics are distinguished is explicitly identified.

Another problem with both conceptual and practical elements is that the term ‘species recognition’ is most often applied when an organism is distinguishing among individuals of a single sex; for example, when choosing a mate [6] or responding to a potential competitor [14]. Yet, species of sexual organisms comprise two sexes. Whether animals recognize both sexes of their own species as a unified category distinct from heterospecifics is a different question from whether they can distinguish between species within a single sex. What defines an acceptable mate for a female is likely to be different than for a male, even though both categories belong to the same ‘species’.

For these reasons, a logical and consistent use of the concept of species recognition will be difficult to achieve. Yet, even were it possible to solve these species problems, prevailing use of the term ‘species recognition’ is further burdened by various additional assumptions, outlined below.

Prevailing assumptions

Species recognition as typology

One simple answer to the question of what animals recognize when endowed with ‘species recognition’ is that they are recognizing a compatible mate; that is, mates with whom reproduction will result in viable and fertile offspring. Equating species recognition with compatibility recognition probably follows from the widespread adoption of the biological species concept (BSC), the most commonly held model of the species entity [5,12]. The BSC describes species as actually or potentially interbreeding groups of organisms that are reproductively isolated from other such groups. Mayr [5,15] argued that the ‘biological meaning’ of the species boundary is “to serve as a protective device for a well-integrated, co-adapted set of gene complexes”, and that behavioral (i.e. species recognition) barriers are the largest and most important of these devices. Ironically, although the BSC was Mayr’s answer to typological thinking about species, the expectation that all members of a species display species recognition (a concept that Mayr rejected) suggests a form of typological thinking. In fact, the ability to discriminate individuals of one group from

another is itself a phenotype that evolves and not a static property of species.

Nevertheless, the appeal of species recognition under the BSC has now become so ingrained that mating with a heterospecific typically is considered a ‘mistake’, a ‘recognition error’, or an ‘incorrect mating decision’ without any knowledge of the fitness consequences of that decision. Although in many cases data validate the assumption that mating with heterospecifics results in relatively low-fitness hybrids, this assumption has been disproven in numerous systems, as shown by documented evidence of adaptive hybridization [16–19] (Figure 1).

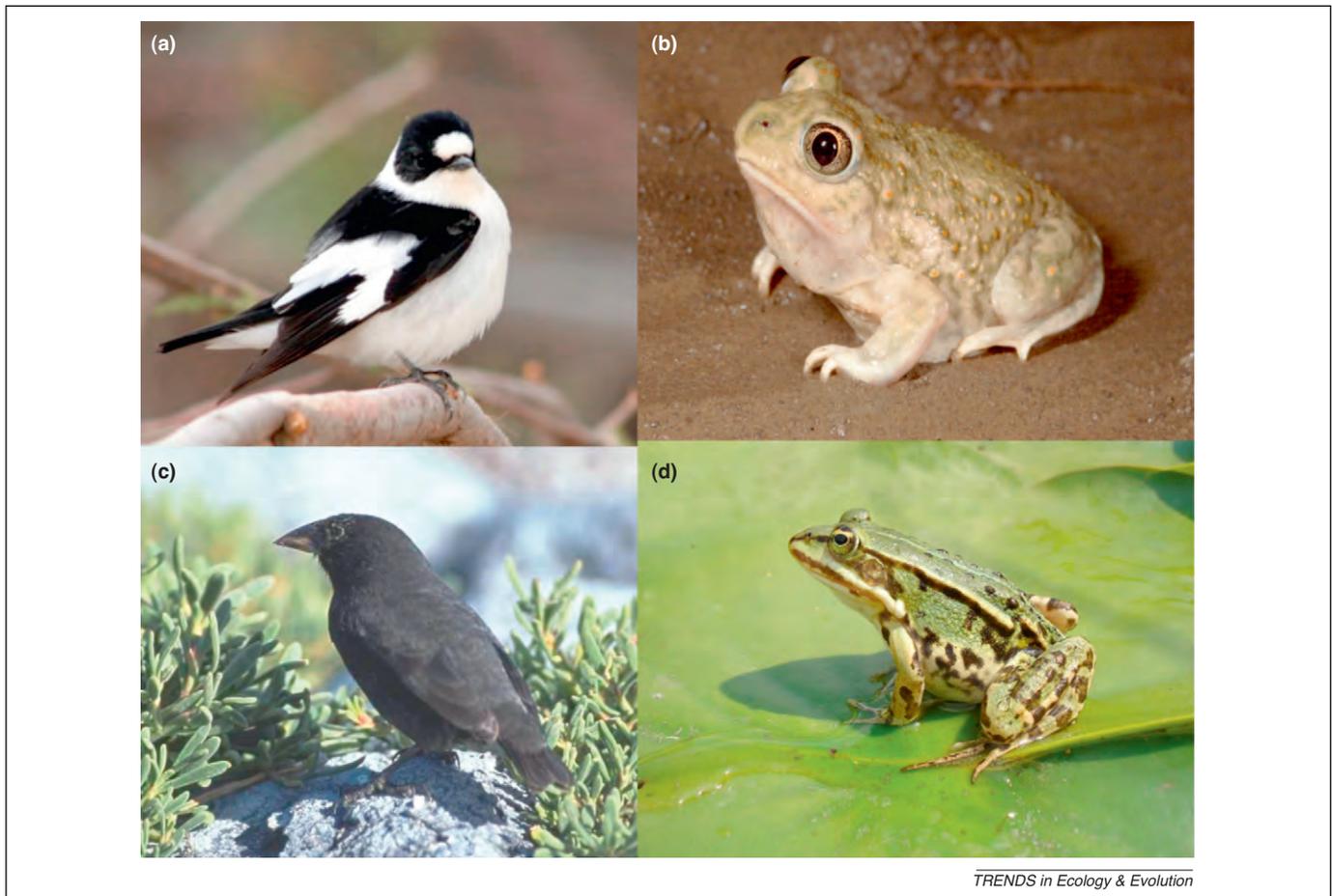
We suggest a fundamental disconnect between theory and practice is to blame for the common assumption that all ‘good’ species are incompatible with others. Despite the powerful theoretical utility of the BSC [12], species descriptions in practice are rarely based on quantitative measures of reproductive isolation, but rather rely on statistical analyses of genetic and/or phenotypic character variation. Although valuable taxonomic characters often include reproductive phenotypes, species taxonomies should be considered hypotheses that are later tested through empirical analysis.

Distinguishing compatibility and quality

Another common practice in the literature on species recognition is to distinguish ‘compatibility’ from ‘quality’ when referring to the attributes of potential mates. A compatible mate in this context might be defined as ‘a mate with whom a focal organism can produce a viable, fertile offspring’, and people often draw on this concept to distinguish conspecifics from heterospecifics (see [20]). Quality, by contrast, is defined as ‘the effect of a mate on the direct and indirect fitness of its partner’, such that a high quality mate is one that provides greater fitness benefits to the receiver. Because ‘compatible’ is often used synonymously with ‘species’ (see above), compatibility becomes a categorical variable, with a potential mate being either compatible (conspecific) or incompatible (heterospecific). Mate quality, by contrast, is assumed to vary continuously within a species.

There are at least two problems with distinguishing compatibility (species) from quality. First, compatibility almost certainly varies continuously, both within and between species. For example, not all conspecific sperm and egg pairs have equal compatibility; numerous studies report intraspecific variation in sperm size, testes size and fertilization success [15,20–22]. Similarly, the assumption that all heterospecific sperm and egg pairings are equally unlikely to be successful is not supported; numerous studies report fertilization success and the production of viable, fertile hybrids among members of different species [16–19].

Second, if we define mate quality in terms of the fitness benefits accrued by the receiver, compatibility is simply one of many ways in which mates can vary along the quality continuum. Thus, compatibility is a subset of quality, representing one of many axes of variation in mate quality. Other axes of quality variation include the degree of parental investment, resource holding potential and indirect benefits such as good genes. Distinguishing a ‘mate quality’ decision from a ‘species’ or ‘compatibility’



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Figure 1. Examples of adaptively hybridizing animal species in nature. (a) Collared flycatcher, *Ficedula albicollis* [17] Reproduced from [http://www.hidephotography.com]. (b) Spadefoot toad, *Spea bombifrons* [16] Reproduced, with permission, from Bill Peterman. (c) Medium ground finch, *Geospiza fortis* [18] Reproduced, with permission, from Guiliano Gerra and Silvio Sommazzi. (d) Edible frog, *Pelophylax esculentus* [19] Reproduced from [http://www.wikipedia.org].

decision therefore implies that some decisions are not about relative fitness. We see this as a false dichotomy. Every mating decision is a mate quality decision, and selection should favor preference alleles that maximize an individual's relative fitness, irrespective of taxonomic hypotheses [23]. If a signaler is incompatible with a receiver, that signaler is a low quality mate relative to that receiver. Selection is expected to favor preference alleles that reduce the response to that signal, increase the response to signals of high quality mates, or both.

Mating decisions might often incorporate multiple axes of quality variation [24]. Singling out the compatibility axis of quality is justified when selection to distinguish compatible from incompatible mates is a major driver of changes in mate recognition systems, as in cases of reinforcement [16,25,26]. In geographically isolated populations with no close congeners, however, for which variation in compatibility is unlikely to be a significant selective agent, the concept of species (compatibility) recognition would not apply. If most speciation occurs in allopatry [5,12], the opportunity for selection due to differential compatibility is limited and a different agent of change must predominate.

Sequential model of mate choice

Finally, another assumption in the literature on species recognition is that animals engage in a sequential process

of mate choice, in which individuals must first choose the right species, and then choose the highest quality mate within their species. A number of problems emerge when examining this hypothesis in light of the arguments made above. The first is the 'species' problem, because the meaning of the term 'species' in this model is unclear from the perspective of the animal. If we attempt to clarify the term by substituting 'compatible mate' for 'species' (i.e. "first choose a compatible mate, then choose a high quality mate"), the problem remains that compatibility is not distinct from quality, but is rather a kind of quality. What is left, then, is a model that describes a mating decision as a chronological process in which individuals first choose a compatible mate, and then choose a mate based on some other indicator of quality variation. In other words, the sequential model posits that signals indicating compatibility are perceived, processed and responded to before signals that indicate some other axis of quality.

It seems clear that different signal components can indicate (or correlate with) different axes of quality [24], one of which might be compatibility in an interspecific context. However, whether compatibility indicators are processed first in a sequence, or even afforded the greatest weight among potentially multiple indicators of quality in a complex signal, is an intriguing hypothesis that has not, to the best of our knowledge, been empirically tested.

Research framework

Our main objective is to understand the role of sexual communication in the origin and maintenance of animal diversity. For decades, the concept of species recognition has held a central place in efforts to achieve that objective; however, for reasons outlined above, we conclude that the concept is hindering our progress. Here, we outline a research framework that does not rely on the concept of species recognition, focusing on the processes that drive changes in mate recognition systems and the phenotypic differences that restrict gene flow between diverging lineages.

The evolution of mate recognition systems

Two general pathways can lead to distinctions in mate recognition behavior between diverging lineages and behavioral isolation. We refer to these pathways as 'endogenous' for processes driven from within a species, and 'exogenous' for processes driven by external factors (both biotic and abiotic). The dichotomy is somewhat artificial because evolution always occurs within a lineage and fitness is always expressed in the context of an environment. Nonetheless, this structure has heuristic value in clarifying alternative processes that lead to changes in mate recognition phenotypes and, ultimately, behavioral isolation.

Endogenous processes are best illustrated by allopatric models of speciation, in which behavioral isolation evolves as a byproduct of evolution in geographically isolated populations, independently of environmental differences [12]. Sexual selection is the process most often implicated in the evolution of behavioral isolation between allopatric populations [7] and is expected to favor courtship traits that provide direct or indirect benefits to receivers [8,27]. In either case, sexual selection can lead to behavioral isolation if signals and preferences coevolve to fixation [28]. Genetic drift is an alternative process appropriately considered endogenous, because evolution occurs due to random sampling of genetic variation within a population. Genetic drift has been hypothesized to cause evolution in sexual traits in founder effect models [29,30].

An important distinction between endogenous and exogenous pathways is that an endogenous pathway, via selection, drift or a combination of the two, can fix differences in mate recognition systems with no influence from other species. By contrast, exogenous pathways to divergence occur as a direct result of differences in biotic or abiotic features of the environment. For example, reproductive interference might occur when the signal values and/or preference functions of two sympatric species overlap, leading to maladaptive behavior in receivers. If receivers that are attracted to heterospecific signals suffer some fitness cost, selection should favor preferences that increase the probability of conspecific mating. Reproductive interference has been discussed in one form or another by various authors [31–33]; we briefly summarize the chief means by which it can operate.

In the case of closely related overlap, two species with overlapping mate recognition systems are so closely related that heterospecific mating is likely to occur, and receivers suffer either direct or indirect fitness costs. If receivers

responding to heterospecific signals suffer reduced mating or fertilization success, sexual selection should act directly to reduce those preference alleles in the population. If hybrids form and themselves suffer reduced fitness, selection on preference alleles is indirect but the effect is similar; this is the classic mechanism of reinforcement [4,34]. In both cases, behavioral isolation increases between the two sympatric species and, potentially, between allopatric conspecific populations, if only some populations experience the overlap [33]. The relative importance of sexual selection versus reinforcement in explaining behavioral isolation is unknown, and the two processes might act together.

In cases of distantly related overlap, two species with overlapping mate recognition systems are so distantly related that heterospecific mating is never attempted; for example, when the signals of singing insects and singing birds overlap in acoustic space. Here, selection on preference alleles can arise due to unproductive mate searching, as confused receivers waste time and are exposed to predation risk in searching for mates. Selection in this case should act directly on signals and preferences to reduce the overlap in signaling space, and behavioral isolation is expected to evolve between allopatric, conspecific populations if only some experience the overlap. Hoskin and Higgie [33] highlight multiple examples of distantly related overlap, including deceptive mimicry [35] and competition for signal space [36].

A third kind of overlap is abiotic overlap, which occurs when features of an animal's mating signal overlap with an abiotic feature of the environment such as rushing water or wind [37]. As in distantly related overlap, receivers suffer search costs because mates are difficult to detect; selection is expected to favor signal variants that do not overlap with the interfering abiotic 'noise', as well as preferences for those variants. As in cases of distantly related overlap and some cases of closely related overlap, behavioral isolation is expected to evolve between allopatric, conspecific populations, only some of which experience the overlap and ensuing selection. Cases of sensory drive [38] provide examples of abiotic overlap.

In addition to reproductive interference, another exogenous pathway proceeds via divergent ecological selection on viability traits that affect mating success, whereby mate recognition systems evolve as a byproduct of adaptation to distinct ecological niches. Here, preferences might evolve due to either direct or indirect selection, creating a context for sexual selection. This collaboration between ecological and sexual selection could drive divergence between allopatric or sympatric populations; examples include preference for body size in divergent ecotypes of fishes and sympatric speciation via 'magic traits' [39].

Although not exhaustive, this framework is intended to inspire various hypotheses by which mate recognition systems might evolve and reduce the probability of gene flow between divergent lineages. Selection to distinguish compatible from incompatible mates is only one of many processes by which preferences for conspecifics can increase. However, when animals are said to use certain signals 'for' species recognition, as commonly noted, the implication is that selection has favored signals and

preferences that distinguish compatible from incompatible mates. In such cases, we suggest that species recognition is better termed ‘compatibility recognition’ and that this hypothesis be rigorously tested before concluding that selection on compatibility variation is driving the evolution of mate recognition systems.

Identifying relevant phenotypes

Identifying the processes that lead to behavioral isolation requires careful characterization of the phenotypes involved [2]. A consensus view in the literature suggests universal characteristics of ‘species recognition’ signals to be: fixed in a species; unique to a species; and necessary for attracting a compatible mate. These types of signals are of fundamental interest because they are likely to represent the signal differences responsible for behavioral isolation, but referring to them as species recognition signals is not constructive for the reasons outlined above. Of these three characteristics, we are particularly interested in signals that are a prerequisite (*sine qua non*) for attracting a compatible mate. We refer to these as necessary mate recognition signals, and we hypothesize that when necessary signals are fixed in and unique to a given species, differences in these signals contribute to behavioral isolation.

Necessary recognition signals are traits, or combinations of traits, that must be present to elicit mating from a compatible member of the opposite sex. Identifying a necessary recognition signal requires either removing it entirely from a display—if this eliminates a mating response, the signal is necessary—or manipulating its value and testing for thresholds of acceptability, which can determine a range of necessary signal values [40]. Necessary signals could vary categorically or continuously; for example, a ‘red’ belly might be necessary to elicit a mating response, but a range of values of ‘red’ might be acceptable.

Importantly, this use of the term ‘species recognition’ is independent of evolutionary process, and rather appears to describe a certain class of signaling phenotypes. Necessary recognition signals presumably evolve due to any of the processes outlined above, so it is important to disentangle common uses of the term ‘species recognition’, which differ with respect to proximate and ultimate assumptions. When used to mean compatibility recognition, species recognition assumes an ultimate cause, in this case an exogenous process (i.e. reinforcement). By contrast, necessary recognition signals describe a functional, proximate class of phenotypes with no reference to the underlying process. If, over time, compatibility indicators become a necessary prerequisite for mating, compatibility and necessary signals might be one and the same, but this is not a given. If most speciation occurs in allopatry [5,12], necessary recognition signals are not likely to arise due to the benefits of distinguishing compatible from incompatible mates.

Ultimately, we wish to describe the entire suite of signal combinations that define an acceptable mate (Figure 2). Animals respond not to taxonomic hypotheses but to combinations of signal values that they find attractive to varying degrees. Defining the multidimensional phenotypic space that represents an acceptable mate, understanding how

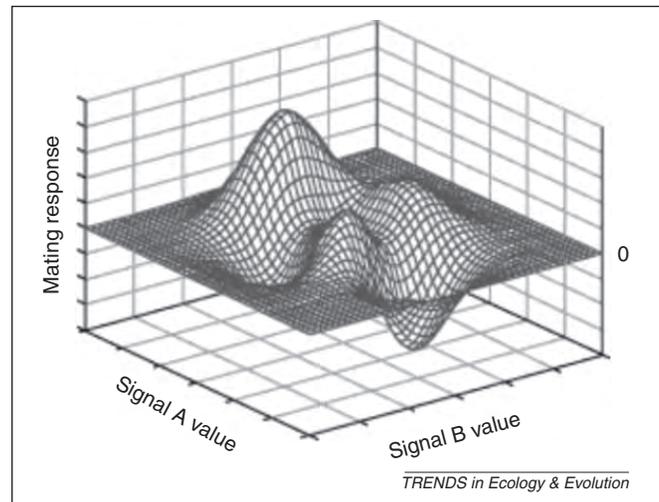


Figure 2. Multidimensional preference space. Two signals that vary from low to high values are represented on the x- and z-axes, and the degree to which an individual responds with mating behavior is on the y-axis. The center of the y-axis represents zero response. Above the center line indicates an increased probability of mating, below the line a decreased probability of mating, as might occur if selection favors avoiding heterospecifics. The shape of this preference function and the axes of signal variation that define it are likely to differ between males and females. Figure modified with permission from Rodney J. Dyer.

that space changes throughout an organism’s lifespan with ecological circumstances and over evolutionary time, how males differ from females, and how species differ from one another is key to understanding how sexual communication contributes to speciation. Moreover, by measuring the strength of responses alongside the fitness consequences of those responses and the frequency distribution of signal combinations, we can begin to predict how mate recognition systems and the boundaries of mate acceptance will evolve over time [41].

The phenotypic architecture of behavioral isolation

Given that animals are likely to integrate more than two axes of signal variation in mate choice, the heuristic illustrated in Figure 2 is overly simplistic. For practical reasons, we might never entirely map the multidimensional phenotypic space that represents an acceptable mate. Nonetheless, meaningful signal differences between species – signal differences that result in reduced gene flow and ultimately the maintenance of diversity – can be identified by examining the phenotypic architecture of behavioral isolation. In particular, which signal differences restrict mating between heterospecifics? We hypothesize that these represent differences in necessary mate recognition signals and contribute to the multidimensional axes shown in Figure 2.

Identifying signal differences that contribute to behavioral isolation is not trivial and requires creative experimental design; many signals might differ between two focal species, and only a subset of these may contribute to behavioral isolation. Here, we outline five experimental conditions that should be met to identify signals that might contribute to behavioral isolation between species (Box 1). Some of the most well supported examples of signals that play a substantial role in behavioral isolation include pheromone composition in moths [42], spiders [43] and *Drosophila* [44], wing coloration in butterflies [45–48]

Box 1. Experimentally identifying signal differences that contribute to behavioral isolation

- Receivers must respond preferentially to conspecific over hetero-specific values of the signal in question. (Although this criterion might seem obvious, it is remarkable how many signals have been identified as contributing to behavioral isolation simply because they differ between species).
- Candidate signals should be presented to receivers embedded within the full array of realized signals. (In behavioral trials, the system should be manipulated such that all variables [i.e. signals] are held constant except those whose effect is to be measured).
- Only the signals of interest should be manipulated. (Manipulating only the signal value of interest can be difficult, because manipulating one signal can inadvertently affect another. For example, preventing a signaler from expressing one element of its normal sequence of courtship behavior might alter its subsequent behavior).
- The mate-choice design should reflect natural social conditions. (Social cues and the opportunity to compare several signalers at once might [or might not] be an integral part of a receiver's mating decision, and mate choice has been shown to vary with the social demography of the testing regime [53,54]. A mate choice design that mimics natural social conditions will provide the most relevant results).
- Receivers should express their mate choice by mating. (Mate choice studies often confine one sex to an inaccessible chamber to control for intrasexual competition. This experimental design does not allow receivers to conclusively demonstrate their mate choice and may preclude the exchange of critical signals that affect mating decisions, for example tactile cues).

and damselflies [25], nuptial coloration in fish [49,50] and frogs [51], and acoustic behaviors in insects and frogs [52]. As these signals become convincingly demonstrated across a range of taxa, universal characteristics or general principles can emerge, and the forces that drive their evolution can be tested.

Conclusion

Our aim is to highlight the ways in which the term 'species recognition' can be confusing or misleading. These include assumptions that are necessarily inherent (the 'species problem') and unnecessarily inherent (that heterospecifics are incompatible, that compatibility differs from quality, that mate choice is based on a sequential algorithm with compatibility indicators processed first) to a concept of species recognition. We outline what we hope is a constructive framework for investigating the evolution of mate recognition systems and its role in the origin and maintenance of animal diversity. Our framework emphasizes the fitness consequences of a mating decision irrespective of taxonomic distinctions, the multidimensional nature of mate choice, and the types of experiments necessary to identify signal differences that contribute to behavioral isolation.

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