

How sensory drive can promote speciation

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Some of the most spectacular and diverse traits in animals are the signals used to attract mates. Closely related species often differ dramatically in signaling traits, in spite of similarity in other morphological traits. The idea that reproductive isolation arises when male mating signals and female preferences differ among populations is an old one. However, until recently, there was almost no information on what generates diversity in mating signals and preferences. This is beginning to change, with emerging results that highlight the importance of habitat differences in generating this diversity. Such differences in ecology are at the root of one hypothesis for divergence in sexual signaling – sensory drive. The sensory drive hypothesis focuses on how communication systems adapt to local environments and predicts that divergence in communication systems will occur when environments differ. Reproductive isolation can arise as a byproduct of this adaptive divergence in behavior.

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How do new species form? Darwin's mystery of mysteries remains elusive. However, the current pace of research about speciation is uncovering many important clues. One area of active research is how sexual selection might promote the evolution of reproductive isolation. Recent comparative and experimental studies offer support to this long-standing idea [1,2]. But we still have very little understanding of how populations come to differ in male signaling traits and female preferences for those traits. This point is crucial. Understanding the causes of differences in mating traits will illuminate both how sexual selection operates within species and how reproductive isolation evolves between diverging populations.

A central question for sexual selection and speciation research is whether the differences in mating traits among populations are arbitrary or adaptive. If differences are arbitrary, historical events and genetic drift determine mating trait diversity; if differences are adaptive, selection shapes diversity. Fisher's runaway model predicts that both male mating traits and female preferences are, for the most part, arbitrary [3,4]. Consequently, these arbitrary traits are free to vary among populations, and divergence should occur easily [5]. By contrast, the sensory drive hypothesis predicts that both male mating traits and the perceptual systems that underlie female preferences adapt to local environments [6,7]. Divergence occurs because local environments impose selection of varying intensity and direction on mating signals aimed at potential mates and on sensory systems that acquire information on predators, prey and mates. The result can be qualitatively different

mating signals and female preferences in different environments, which can lead to sexual isolation.

Sensory drive is the integrated evolution of communication signals, perceptual systems and communication behavior because of the physics of signal production and transmission, and the neurobiology of perception [7,8]. Speciation by sensory drive is a special case of the long-standing hypothesis that reproductive isolation occurs as a byproduct of adaptation to different environments in allopatric populations [9–12]. With sensory drive, the traits showing adaptive divergence are communication traits rather than feeding or life-history traits. Here, I describe sensory drive and the way in which it can promote divergence in mating traits. I also explore the way in which sensory drive can contribute to the early stages of reproductive isolation and argue for the importance of further work in this area.

Sensory drive

Sensory drive [7,8] is a hypothesis about how communication signals are designed to work effectively. In the specific case of mating signals, the hypothesis explores how signals are best designed to attract mates. According to the sensory drive hypothesis, easy-to-detect signals are likely to be favored. Consistent with this, females (usually the 'choosy' sex) often prefer signals that are conspicuous, such as long feathers, bright colors, complex vocalizations, or bizarre extensions of male morphology, such as horns and eye stalks [13]. Inherent properties of signals, such as their color, intensity, or size, affect signal conspicuousness and detection by females, but so do at least three other interrelated processes: (1) habitat transmission (passage of signals through the habitat); (2) perceptual tuning (perceptual adaptation to local habitat); and (3) signal matching (matching of male signals to female perception). The sensory drive hypothesis describes how these three processes shape the evolution of inherent signal properties [8].

First, habitat transmission arises from the physical interaction of signals with their environment [14]. As signals travel from the male to potential mates, they become degraded by the habitat. The relative conspicuousness of a signal can be strongly affected by how well it transmits through the local environment, that is, how well it can be seen, heard, or smelled from a distance [7,15]. Specific characteristics of signals could be necessary to elicit behavioral responses in conspecific females; therefore, signals that preserve these characteristics after transmission through the habitat

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Table 1. Taxa for which sensory drive is implicated in mating trait divergence or the evolution of reproductive isolation^a

Taxon	Signal										Refs
		Habitats differ in transmission of signals	Signals vary with habitat	Perceptual sensitivity varies with habitat	Signals match perceptual sensitivity	Preference varies with perceptual sensitivity or habitat	Divergent signals correlate to R.I.	Divergent preferences correlate to R.I.	Low levels of genetic divergence		
Vogelkop bowerbirds <i>Amblyornchus inornatus</i>	Bower shape and decoration color	Y	Y	U	U	U	U	U	U	Y	[38]
Warblers <i>Phylloscopus</i> spp.	Color patches	Y	Y	U	U	U	U	U	U	N	[26]
Cricket frogs <i>Acris crepitans</i>	Call	Y	Y	P	Y	P	P	P	P	Y	[30,43] [24,29]
Lizards <i>Anolis</i> spp.	Dewlap color	P	P	N	P	U	Y	U	U	N	[44–47]
<i>Anolis cooki</i> and <i>A. cristatellus</i>	Dewlap color	Y	Y	Y	Y	U	U	U	U	Y	[48]
Haplochromine cichlids <i>Haplochromis</i> spp.	Color	Y	Y	Y	P	P	Y	Y	Y	Y	[49–51]
Threespine stickleback <i>Gasterosteus</i> spp.	Throat color	Y	Y	Y	Y	Y	Y	Y	Y	Y	[39]
Snappers (Lutjanidae)		Y	U	Y	U	U	U	U	U	U	[27]
Ermine moths <i>Colias eurytheme</i> , <i>C. philodice</i>	Pheromones	U	U	P	Y	P	P	P	P	N	[52]
<i>Drosophila mojavensis</i> , Baja and Sonoran populations	Epicuticular hydrocarbons	Y	P	U	P	P	Y	Y	Y	Y	[53–57]
Wolf spiders <i>Schizocosa ocreata</i> , <i>S. rovneri</i>	Vibration pattern and leg tufts	Y	Y	P	Y	Y	P	P	P	Y	[58–60]

^a Columns correspond to predictions of the hypothesis that sensory drive promotes speciation through divergence of mating traits and concomitant reproductive isolation. Key: Y, yes; N, no; P, possible but unconfirmed; U, unknown or no data; R.I., reproductive isolation.

are more likely to attract females for mating [16]. In addition, degradation blurs signals, for example by increasing the bandwidth or slightly altering the duration of a clear tonal call, or obscuring the brightness or altering the hue of a color patch. Degradation reduces discrimination efficiency. Degraded signals can increase error rates if females base mating decisions on variation in signal form, because signal degradation decreases the perceived differences between signals given by different males. Because of these varied effects, communication signals are expected to evolve in response to the physical features of the signaling environment.

Second, the habitat can affect not only signal transmission and detection, but also female perception (the ability to see, hear, feel, or smell mates) and also detection by predators and prey. Perception is likely to be shaped by selection acting outside the context of mate choice, for example in the context of finding food [17] or detecting predators, which might be cryptic rather than conspicuous [18–20]. Because of local adaptation in perception (perceptual tuning), females are more sensitive to some sound frequencies, wavelengths of light, or smells than they are to others. The structure of peripheral sensory organs [21] and the organization of the central nervous system can affect the way in which perceptual systems evolve in response to such selection pressures.

Third, signal conspicuousness depends not only on transmission physics, but also on how well the signal is matched to receivers' perception (signal matching). For example, females can hear a tonal call that is at their frequency of greatest sensitivity at lower amplitude than they can hear a call that is far offset from this frequency [14]. Thus, males producing closely matched

signals can be detected from farther away. This can increase male mating success, because more females can detect the males. It might also reduce female search costs by decreasing the time required to detect potential mates [22]. Ease of detection can benefit both males and females; consequently, closely matched signals are likely to be favored over less well-matched signals.

Taken together, the three processes of sensory drive (habitat transmission, perceptual tuning, and signal matching) can cause female perception and male signals to coevolve. This might occur because they are shaped by similar environments, or because close matching increases the effectiveness of communication.

Divergent selection via sensory drive

Sensory drive describes the action of both natural and sexual selection on signaling systems [7,8]. Natural selection acts directly on signals via habitat transmission and directly on perception via perceptual tuning, and sexual selection acts indirectly on signals via signal matching. When local environments differ, the action of selection on signals and perception will also differ, which could lead to divergence in mating traits. Here, I describe the way in which divergent natural and sexual selection can lead to divergence in mating signals, perception and preference.

Habitat transmission is likely to vary with structural features of the habitat [14]. Thus, a signal that transmits well in one habitat can be heavily degraded in another [23,24], leading to possible divergence among mating signals in populations from different habitats [25] (Table 1). For example, old-world *Phylloscopus* warblers that live in low light habitats display brighter color patches than do those that live in

Box 1. Terrestrial light environments and spectral sensitivity

Environmentally tuned spectral sensitivity appears much rarer in terrestrial taxa than in aquatic taxa [a], perhaps because the 'color' of terrestrial light environments is less distinct or more variable over time [b] unless habitats are quite different (e.g. forest versus desert or night versus day). However, not all three components of sensory drive (habitat transmission, perceptual tuning, and signal matching) are required for it to contribute to reproductive isolation. Habitat transmission alone can favor sufficiently different mating signals to generate some reproductive isolation. For example, although the amount of light varies for *Anolis* spp. microhabitats in Puerto Rican rainforests (e.g. some are much shadier than others), the dominant color of the background light is green in most microhabitats [c]. Spectral sensitivity shows relatively little divergence among species in forest habitat [d], with peak sensitivity at ~550 nm, which matches the green background light [c]. Spectral sensitivity closely matched to background light enhances detection of prey, because objects appear in silhouette against the bright green background. Although green background predominates, the color of the substrate against which males display does vary. Females respond most strongly to dewlaps that move and that contrast in brightness against the substrate [e]. Dewlap color is involved in mate recognition and contributes to reproductive isolation [f]. Dewlap colors are conspicuous in their own habitat but less so in the habitats of other species [e]. For most *Anolis* spp., it appears that habitat transmission in the absence of perceptual divergence has shaped differences in male dewlap colors among many closely related species. Sensory drive has played a role in this but probably did not initiate the evolution of reproductive isolation here; the divergence in dewlap colors is likely to have followed ecological divergence and habitat preference [g].

However, perceptual tuning appears to have a more direct role in the evolution of reproductive isolation for two closely related and ecologically very similar species, *A. cooki* and *A. cristatellus* [h]. *Anolis cooki* occupies sparsely vegetated, dry habitat with bright, broad spectrum background light rich in UV, whereas *A. cristatellus* occupies more densely vegetated habitat with green background light. *Anolis cooki* are less sensitive to UV light than are *A. cristatellus*, and their dewlaps reflect little UV light, whereas those of *A. cristatellus* reflect strongly in the UV. Thus, *A. cooki* see their own dewlaps as high contrast, but to *A. cooki*, the dewlaps of *A. cristatellus* blend in to the background, because both dewlaps and background are rich in UV [h].

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brightly lit habitats [26], presumably because dull patches are hard to see in the dim light of dense forest.

Differences in habitat can also drive divergence in perception (Table 1). Environments vary in how they mask predators, prey and mates. The actual predators, prey and mating signals can also vary. These multiple perceptual demands might favor different perceptual sensitivity for populations in different habitats to best perform the specific detection tasks posed by the local environment [19]. For example, correlations between water color and spectral tuning (colors to which eyes are most sensitive) are well known in fish. Snappers (Lutjanidae) that live in the clear, blue water of outer shelf reefs have rhodopsins with sensitivity shifted to the blue end of the spectrum [27]. By contrast, snappers

that live in yellow–green inshore waters have their sensitivity shifted to the green part of the spectrum. Spectral tuning matches quite closely the predicted optima for the respective environments of the snappers [27]. Unfortunately, data on mating behavior in these species are unavailable, so it is unknown whether mating signals match this variation in perception. Although spectral tuning is well known in fish, differences in color vision and color signals contributing to reproductive isolation might be much more likely in aquatic organisms than in terrestrial ones (Box 1).

Because signals that match perception are likely to be favored, divergence among populations in perception is another source of divergent selection on male signals (Table 1) [28]. For example, the sound frequencies to which female cricket frogs *Acris crepitans* are most sensitive differ among populations [29]. The dominant frequencies of male calls differ in a correlated fashion [30]. Thus, female perception and male signals are closely matched [29]. The populations studied inhabit different environments, and both perception and signals vary in correlation with environmental differences [30].

A pleiotropic effect of evolution in perception is change in the preference that females express for male signaling traits (Table 1). To the extent that mate preference depends on what is best seen, heard, smelled or felt, perceptual variation can contribute to divergence among populations in female preferences (Box 2).

Sensory drive and the evolution of reproductive isolation
Because mate preferences and signals adapt to local environments and coevolve by the mechanisms described above, populations in different environments will diverge in mating traits (Table 1). Even small differences in the environment can have substantial effects. Divergent or mismatched signals and preferences reduce the probability of mating between populations because females in one population prefer a particular signal and males in a second population display another; this interferes with mate recognition. The greater the divergence in male signals and female preferences, the greater sexual isolation will be.

The process of divergence in mating traits can occur between populations, driving early divergence of lineages, or, between species, maintaining existing independence of lineages. Sensory drive is most likely to play an important role in speciation for allopatric populations that come into secondary contact, because of the pivotal role of habitat differences in driving divergence in mating traits and the greater likelihood of habitat differences in allopatry. Mating traits that have diverged in allopatry via sensory drive are more likely to maintain reproductive isolation on secondary contact if populations sort themselves into different microhabitats for breeding. This enables sensory drive to continue to operate differently on the two populations. Several factors can cause habitat segregation, including competition for resources, breeding territories or enemy-free space [12].

Box 2. Case study of sensory drive and reproductive isolation: lake-dwelling sticklebacks

Threespine sticklebacks *Gasterosteus* spp. invaded the coastal lakes of British Columbia after the last ice age and diverged from their marine ancestors in the ensuing 12 000–15 000 years [a]. Drainages are isolated and, thus, this evolution has been largely independent [b] and has resulted in divergence in male mating signals. In some lakes, males display the ancestral red nuptial color, whereas in other lakes males display black [c]. Among the red populations, there is substantial variation in both the intensity and extent of red. Red and black sticklebacks are even found together in one lake – the limnetic males are red and benthic males are black [a,d]. Sensory drive is an important mechanism of divergence in male mating signals, female perception of color, and preference for red males, and contributes to reproductive isolation between populations differing in these sexually selected traits [e].

Nesting habitats of stickleback populations differ in water color – typical water color is greenish, but several lakes have red shifted water [c,f]. In addition, blue wavelengths are attenuated with depth, making deeper water more red shifted even in the greenish lakes [e]. Benthics nest in deeper and more densely vegetated areas than limnetics, thus, they nest in more red-shifted habitat. Red nuptial color should be masked by the red-shifted light, because of reduced contrast of the signal against the background [g]. Male benthics and solitary populations that nest in red-shifted habitats display black nuptial color or reduced red [c,e]. Female sensitivity to red light is shifted to longer wavelengths [f] or is lower in populations that nest in dimmer, red shifted habitats, and male signals match this spectral tuning [e]. This matching might arise because of coevolution between male signals and female perception, or because both have adapted to the same local habitat. Perception and preference are correlated: females with low sensitivity to red light express no preference for red males; females with high sensitivity express strong preferences for red males [e]. The extent of divergence in both male signals and female preferences correlates with the extent of reproductive isolation [e], indicating that divergence in these sexually selected traits contributes to speciation.

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Sensory drive itself can guide habitat choice [7] if microhabitats vary in transmission properties and the optimal microhabitat differs among populations because of divergence in signals or perception. Then, males from two populations might choose different microhabitats to facilitate signal transmission [16], or females might choose different habitats, in which they can see or hear mates, food and predators well [31]. Males can also choose different breeding habitats, in which their signals are cryptic to predators or where predators that can readily perceive their signals are absent [31,32]. Males might also shift to breeding at different times of day to enhance signal transmission [33] or to avoid predators [20]; this can create temporal isolation.

If allopatric populations in secondary contact do not segregate into different microhabitats, selection on signals and preferences is unlikely to remain

divergent. Initial divergence might collapse, and the two populations could fuse to form a single species. If reproductive isolation is maintained, it will no longer depend on sensory drive, although it could depend on trait divergence caused by sensory drive in allopatry. That is, mating traits could be sufficiently different at the point of secondary contact to generate assortative mating. If the traits are not costly, the derived state might be retained on secondary contact and continue to contribute to reproductive isolation. The speciation process might go to completion by other processes, such as competition for resources and associated divergence in ecological and morphological traits. In this scenario, the importance of sensory drive in speciation is limited to the allopatric phase.

Divergence in perception need not be driven by direct selection. Perception can evolve as a correlated side effect of another trait under selection, or it can differ between populations by chance. Frogs provide a reasonable hypothetical example. The sound frequency to which females are most sensitive depends on body size in many frog species, as does the dominant frequency of male calls [34]. Larger frogs are most sensitive to lower frequency sounds and give lower frequency calls. Suppose allopatric populations evolve to different body sizes because of prey distributions. These populations probably also differ in frequency tuning of both female ears and male calls. The result could be reproductive isolation between descendent populations if they have nonoverlapping perceptual or call frequency distributions. Any resulting reproductive isolation would be a byproduct of adaptation to different environments, although neither perceptual adaptation nor habitat transmission of calls drove the divergence.

Conclusions

Can speciation occur by sensory drive alone? Evolution of sexually selected traits is likely to be both rapid and dynamic [2,6], setting the stage for sexual isolation to evolve. Yet, ecologically similar species are unlikely to coexist, even when some sexual isolation exists. Concomitant changes in ecological traits might be necessary for coexistence on secondary contact so that one species does not exclude the other [12]. Speciation is therefore most probable when ecological and mating traits diverge hand-in-hand.

How often does divergent selection lead to reproductive isolation? This is not yet known, but there is evidence that natural selection contributes to reproductive isolation in natural populations [35,36]. Evidence is emerging that sexual selection also plays a role [37–39]. Thus, to fully understand the role of selection in speciation, studies of natural and sexual selection need to be integrated. Sensory drive can serve as a pivot point for that integration, because the hypothesis focuses on how ecology affects the action of both forms of selection on mating traits.

The sensory drive hypothesis highlights the importance of considering the ecological context in

Box 3. Sensory drive and condition dependence as complimentary modes of mating trait divergence

Easy detectability of signals should reduce female search costs, but sensory drive does not provide a complete set of predictions for the evolution of female preference when males vary in the direct or indirect benefits they provide to females. Preexisting bias also ignores predictions that female preferences should evolve to optimize female reproductive success [a]. Even if a particular male signal elicits high sensory response in females, mate choice should depend on that signal only if the preference carries low cost or is beneficial, so beneficial preferences are expected to be more common. Male ability to exploit preexisting biases would thus be constrained. Signal and preference evolution are likely to depend not only on signal detection and sensory stimulation, as predicted by sensory drive and preexisting bias, but also on processes postulated by condition-dependent handicap hypotheses [b,c]. Exaggeration of male traits through the runaway Fisher process is unlikely to be simultaneously integrated with sensory drive, because natural selection on female perception can result in costly female choice, retarding the runaway. However, sensory drive could initiate preferences for signals that might be further exaggerated by runaway if selection on preference is relaxed.

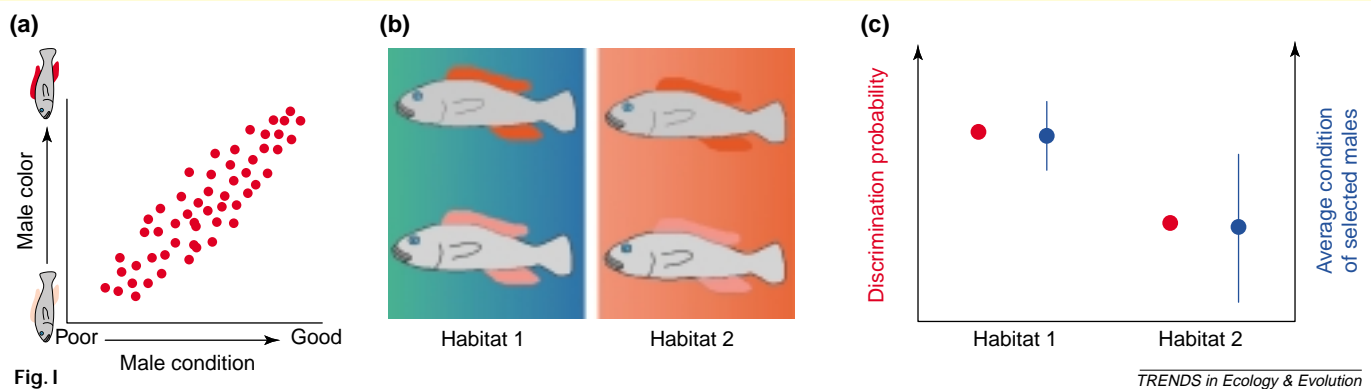
Transmission of signals through habitat can affect the perception of the signal, the ability to discriminate between signals, and consequently, the average condition of selected mates. In Fig. 1a, the intensity of male fin color covaries with male condition. Males in good condition display intense color, whereas males in poor condition display pale color. Thus, color is condition dependent and can be used by females to select males in good condition. In Fig. 1b, transmission through the habitat affects perceived differences between males and can undermine discrimination between intense and pale color. In habitat 1, a small amount of degradation occurs, and females are still able to discriminate intense from pale males. Thus, the average condition of the males that are selected as mates by females is high, with small variance (Fig. 1c). In habitat 2, substantial degradation takes place, obscuring differences between intense and pale color. Females are more likely to make errors and select pale males, resulting in lower average condition of selected males and higher variance in condition (Fig. 1c).

The reduction in average condition poses a cost to females, and the increase in variance reduces both the covariance between preference and signal and the strength of sexual selection. Thus, in habitat 2, preferences for alternative male traits could evolve.

Sensory drive predicts signals that transmit well through the local habitat [d] are likely to evolve as condition indicators because preferences for those traits are likely to increase female fitness. Therefore, when environments differ, sensory drive and condition dependence interact synergistically to cause divergence in signals and preferences. A logical (although not necessary) outcome of this process is sexual isolation between populations that have adapted to different signaling environments. It is already known that sensory drive, condition dependence, and Fisher's runaway process are not mutually exclusive [e,f]. However, little work has tested these hypotheses jointly or investigated the manner in which they might interact (but see [d,g]). Such joint investigation is likely to prove fruitful.

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which sexual selection operates, even when signals and preferences are condition dependent (Box 3). The unique role of ecology postulated by the sensory drive hypothesis is not on how exaggerated a male signaling trait becomes under the joint action of natural and sexual selection. The hypothesis does make predictions about this, but so do the Fisher process and indicator trait models [4,40]. Rather, the novel perspective of sensory drive is on which traits are used as mating signals and on how different environments might favor qualitatively different traits, rather than simply a more-or-less exaggerated form of one trait.

Prospects for research

Sensory drive has the potential to be an important factor in speciation, yet many questions remain. How robust is

sensory drive when female preference or male signals carry a cost? Is divergent sensory drive alone sufficient to produce reproductive isolation among populations in different habitats, and under what conditions? Does divergent sexual selection via sensory drive or divergent natural selection on ecological traits contribute more often to reproductive isolation? How does ecological divergence or genetic incompatibility affect the likelihood or rate of speciation initiated by sensory drive?

Progress in addressing these questions will be facilitated by comparing populations in different habitats for all three components of sensory drive and then estimating the levels of reproductive isolation that arise from divergence in signals and preferences (Table 1). Extensive data exist on perceptual or signal variation for some taxa but, unfortunately, few data are

available on the extent of reproductive isolation among populations or closely related species for these same taxa. Comprehensive study of carefully selected taxonomic groups and taxa that use varied sensory modalities would be fruitful. This would require incorporating methods from the diverse fields of animal communication, neuroethology, behavioral and evolutionary ecology, and genetics, and so would require broadly trained scientists or extensive collaboration.

Sensory drive is primarily a verbal model. Theoreticians could contribute importantly to further development and testing of the hypothesis by explicitly modeling its processes in an integrated way. Models should incorporate the physics of habitat transmission [41], signal detection and perceptual evolution [14], perhaps with neural networks [42]. Such models would allow an evaluation of the range of conditions under which sensory drive might lead to speciation.

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