Comparative evaluation and its implications for mate choice

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Experiments on decision making by humans show that the choices that we make can be very labile. The magnitude of our preferences, and even our rank ordering of options, can vary according to the number and type of alternatives available for comparison. This apparent irrationality has been argued to result from our use of decision heuristics that have evolved to enable us to choose quickly and efficiently between options differing in multiple attributes. Here, we argue that, because there is also selective pressure for animals to make mating decisions quickly, and because potential mates also differ in multiple attributes, similar decision heuristics might have evolved for mate choice. Following this reasoning, the attractiveness of a given mate will depend on the others with whom he or she is being compared, rather than being an absolute function of his or her underlying quality. We describe some of the ramifications of such comparative evaluation, and argue that it could offer new insights into some of the biggest outstanding problems in mate choice and sexual selection.

Mate choice as information processing

Mate choice can be viewed as an information-processing problem [1]. Females have to perceive cues from males; they have to remember this information from one male to the next; and, finally, they have to use the information that they have obtained to make mating decisions (Figure 1). In contrast to the many studies identifying the cues that females attend to in males and the underlying qualities signalled by these cues [2], there has been less empirical work directed at understanding
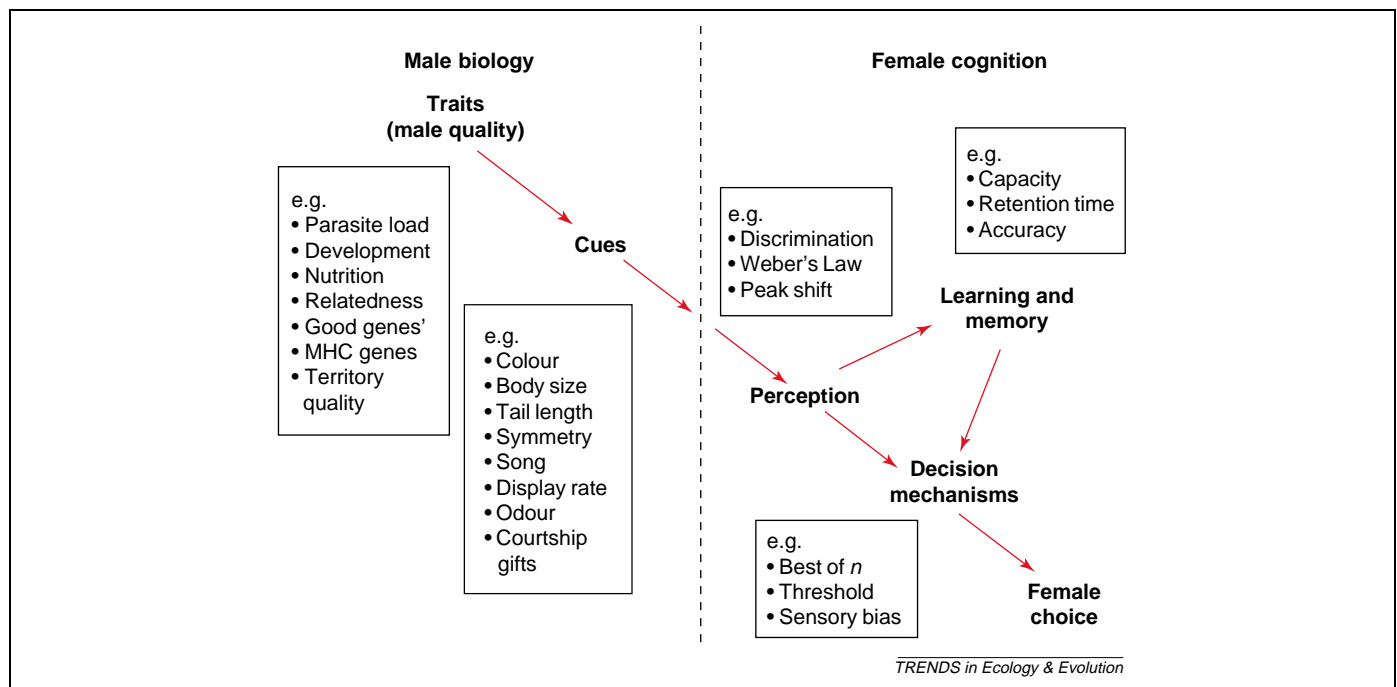

Figure 1. The flow of information from the male to the behavioural output of the female. The assumption is that male quality translates into his traits, which then serve as cues for the female [42]. Her choice is based on her ability first to perceive the trait(s) of the male and then to use that information to make her decision [43]. The information from one male will be compared with that she has received from other males, and this comparison will be affected by her cognitive abilities, including her memory, and her ability to process information from multiple sources simultaneously.

the role that female cognition has in mate choice. Whereas some consideration has been given to the possible influences of perceptual mechanisms in mate choice [3–5], less has been given to the problem of how decisions are made once information has been obtained [2]. This task is complicated by the fact that sexual displays often comprise multiple cues that, in many cases, appear to provide information about different underlying qualities [6]. Furthermore, these qualities are not necessarily positively correlated [7–9], creating the need for females to trade off conflicting attributes in males [10,11]. The implicit assumption adopted in most models of mate choice is that cognitive mechanisms can be justifiably ignored, because if there are selective advantages to be gained from mating with specific males, then females will have evolved the neural machinery necessary to identify these males accurately [12].

However, we argue here that the decision mechanisms used by females deserve closer scrutiny. Evolutionary tradeoffs between the efficiency of decision making and the accuracy of resulting choices are likely to have resulted in mechanisms that are based on comparison of the alternatives available rather than on an absolute standard. Such mechanisms would result in predictable, but not previously considered, biases in mate choice, and consequently predictable adjustment in male signalling strategies. Here, we review the evidence for comparative decision-making heuristics, and consider the significance that their existence might have for mate choice and sexual selection.

The psychology of human judgment and decision making

Researchers of decision making in humans have for some time been interested in the problem of how we make choices when the available options differ in more than one attribute. This problem is particularly acute in so-called 'unfriendly' choice environments [13], where different attributes are negatively correlated such that no single option emerges as dominant (i.e. either as good as the others or better on all attributes). Such choices are frequently encountered by consumers because price and quality are usually positively correlated within any product range. Normative models of human behaviour assume that consumers should combine all the relevant attributes to obtain a single absolute measure of value for each option that is independent of the other options available, and choose the option with the highest overall value. This approach should result in choice behaviour that exhibits properties of economic rationality [14], such as transitivity and independence from irrelevant alternatives (IIA). Formal definitions of these concepts are given in Box 1, but put simply, they both imply that, all else being equal, decisions are consistent across different choice contexts.

However, an extensive empirical literature on decision making in humans suggests that we are irrational, frequently displaying violations of transitivity and IIA. These violations are prevalent when the choice involves options that differ in more than one attribute and, specifically, when the supposedly irrelevant alternative added

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Box 1. Hallmarks of rational decision-making

Transitivity
Transitivity is a property that applies to a series of binary choices. For example, assume that A is preferred to B and that B is preferred to C, then for transitivity to hold, A should be preferred to C. Preference for C over A is a violation of transitivity. For example, Shafir [21] presented foraging honey bees with a series of binary choices between pairs of artificial flowers varying in depth and volume of nectar contained. He found individuals that preferred flower A to B, B to C, C to D but D to A – a violation of what is known as weak stochastic transitivity. These bees also violated strong stochastic transitivity, which implies that the strength of preference between two flowers adjacent on the scale of utility (e.g. A and B) is larger than that between two more widely separated flowers (e.g. A and C). It is probably significant that Shafir's flowers differed in more than one attribute; violations of transitivity typically occur when humans are faced with analogous multidimensional problems [22]. To date, most experiments directed at uncovering mating preference functions in animals have focused on manipulating single stimulus attributes. To look for intransitivities in mate choice, and hence evidence for comparative evaluation mechanisms, it would be interesting to quantify the preferences of females for a series of males differing in multiple attributes using a paradigm similar to that adopted by Shafir.

Independence from irrelevant alternatives
Independence from irrelevant alternatives (IIA) is a property that applies when a choice set is expanded. It implies that the preference between two options should be independent of the presence of additional inferior alternatives. For example, given the binary choice of A and B, assume that A is preferred to B. If an inferior option C is then introduced into the choice set this should not affect the preference for A over B. If the relative preference for A over B is altered by the addition of C, this is referred to as a violation of the constant ratio rule. If the absolute preference for either A or B increases when C is added, this is referred to as a violation of regularity. Violations of regularity are regarded as strong evidence for the existence of comparative evaluation mechanisms [18]. To look for violations of IIA in mate choice, it would be necessary to quantify female preference for the same pair of males in the presence and absence of another male (or males). If the preference for a given male increases when the number of males in the choice set is enlarged, then this would be evidence for comparative evaluation mechanisms.

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to the choice set is what is known as an asymmetrically dominated decoy (ADD) [15–17]. Consider a choice between two options designated the 'target' and the 'competitor', where the target is high on one attribute and the competitor high on the other. When an inferior ADD option is introduced that is dominated by the target on both attributes but by the competitor on only one, a common finding is that the preference for the target increases. We henceforth refer to this violation of regularity as the 'ADD effect'. To give a real example, purchases of large cans of a high-quality, high price brand of baked beans (the target) increase, and purchases of large cans of a low-quality low price brand (the competitor) decrease, when smaller, relatively more expensive cans of the high-quality brand (the decoy) are added to the choice set [16]. This is a violation of regularity because preference for the target option increases when the decoy is introduced.

The violation of regularity that occurs when an ADD is added to a choice set is incompatible with the assignment of absolute values to items, and instead requires that an item is evaluated relative to the other items available at

the time a choice is made [18]. The crucial distinction between absolute and comparative evaluation is that, whereas absolute mechanisms enable valuation of an option in isolation, value is only defined in comparative mechanisms relative to the other options with which an option is compared. These other options need not necessarily be simultaneously present because details of past encounters can be stored in the memory of the individual concerned. Several specific comparative evaluation mechanisms have been proposed [19] and we give two example mechanisms in Box 2.

Why has comparative evaluation evolved?

Decision heuristics based on comparative evaluation might have evolved because they facilitate decision making, particularly when options differ simultaneously in two or more attributes (such as price and quality) [20]. It is cognitively easier to compare alternatives separately on each attribute dimension, rather than trying to arrive at an absolute evaluation for each option based on all of its properties [21,22]. Thus, although comparative evaluation can sometimes result in irrational behaviour, the fitness costs resulting from the occasional choice of a suboptimal option are assumed to be offset by either the time or

neural-processing machinery saved by the adoption of cognitively simpler heuristics.

Empirical evidence from animals for comparative evaluation

Comparison appears to be a general property of perception [23,24]. It is well known that the perception of the magnitude of a stimulus is affected by comparison with other simultaneously available stimuli (Figure 2), as well as by the memory of previously experienced stimuli (also known as 'background context') [25]. For example, rats respond differently to an identical food reward depending on whether they were previously given a smaller or larger reward in the same task [26], a phenomenon referred to as a 'contrast effect'.

Recently, a few studies in the foraging literature have asked whether ADD effects occur in animals, with the aim of establishing whether animals are using comparative evaluation mechanisms to make complex multidimensional decisions. Results show that the preferences of animals choosing between foraging options differing in two dimensions (e.g. the volume and concentration of nectar contained in an artificial flower) can be manipulated by the addition of decoy options to the choice set in a

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Box 2. The asymmetrically dominated decoy effect

Sedikides *et al.* [17] provide an example of the asymmetrically dominated decoy (ADD) effect in human partner selection.

In the study, three groups of students were asked to indicate their preferred partner from each of several sets of eligibles described according to their percentage points on a range of attributes including physical attractiveness and sense of humour (Figure Ia). In the binary group, the sets comprised pairs of eligibles (A and B), whereas in the two trinary groups, the sets comprised trios consisting of the same two eligibles present in the binary sets with the addition of a third eligible (C_A or C_B), the values of whose attributes were such that the eligible constituted an ADD designed to increase the attractiveness of either eligible A (in the trinary group with C_A) or eligible B (in the trinary group with C_B).

The percentage of students choosing eligible A increased relative to the binary treatment in the trinary treatment with C_A, and decreased relative to the binary treatment in the trinary treatment with C_B (Figure Ib). Thus, the relative attractiveness of eligibles A and B is dependent on the context in which they are presented. (Figure I based on data from [17].)

Possible mechanisms underlying the ADD effect

(i) The ADD effect could result from the perceptual effects of altering the range of stimuli along each of the attributes of interest. Specifically, a given difference between two points on a stimulus dimension is perceived as smaller when it is embedded in a bigger range of values [24]. The result is that the discriminability of two stimuli can be affected by the context in which they are presented. By definition, an ADD extends the range of the attribute for which the target is inferior to the competitor, reducing the perceptual difference between the target and competitor in this attribute, and therefore downplaying the disadvantage of the target relative to the competitor. In the above example, male C_A has a lower sense of humour than either males A or B, and therefore has the perceptual effect of reducing the subjective difference between A and B in sense of humour. This could raise the overall value of A relative to B because male A's higher attractiveness now becomes more salient.

(ii) Alternatively, the ADD effect could result from the decoy altering the so-called 'dominance relationships' of the target and the competitor. In the absence of the decoy, neither the target nor the competitor is dominant to one another. However, the ADD breaks this deadlock in
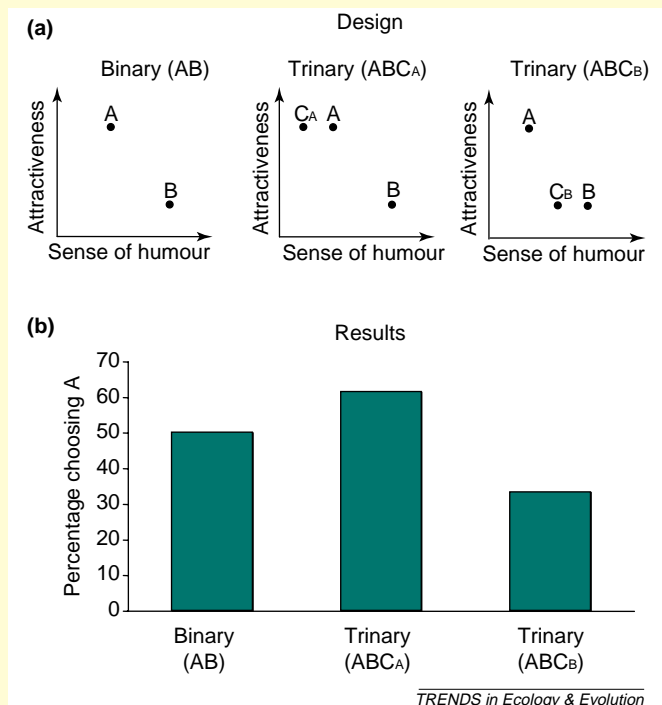

(a) Design

Binary (AB)   Trinary (ABC_A)   Trinary (ABC_B)

(b) Results

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Figure I.

favour of the target because the target is now dominant to the decoy on both attributes, whereas the competitor is only dominant to the decoy on one of the attributes. In the example above, in the binary treatment male A and male B both win on one attribute, A is more attractive, but B has a better sense of humour. However, when male C_A is added to the choice set, he increases the overall value of male A relative to male B because A is dominant to C_A on both attractiveness and sense of humour whereas B is less attractive than C_A (Figure I).
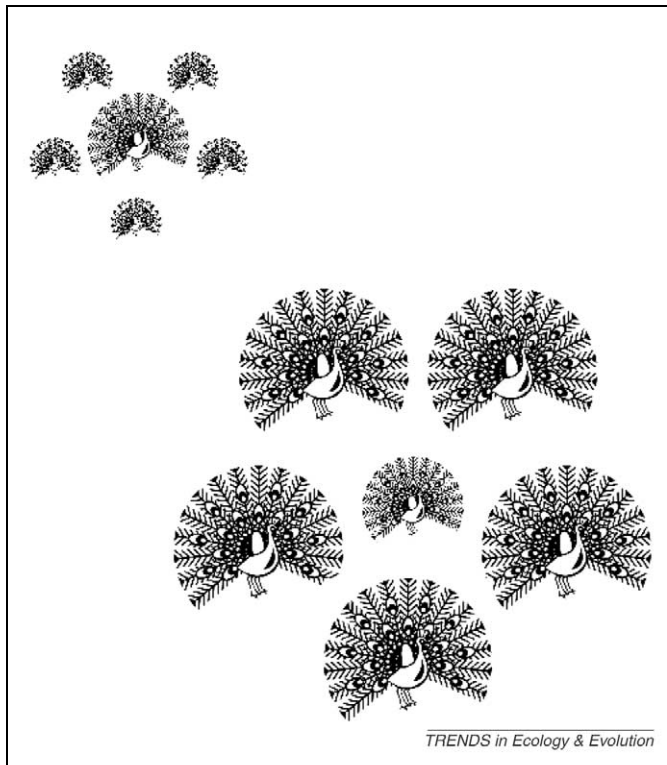
Figure 2. A version of the Ebbinghaus–Titchener illusion: a striking example of comparative evaluation in visual perception. The two central peacocks are the same physical size, but appear to be different sizes as a result of the birds surrounding them.

manner that is similar to the effects described in humans. It has been demonstrated that, in honeybees *Apis mellifera*, rufous hummingbirds *Selasphorus rufus*, and grey jays *Perisoreus canadensis*, it is possible to shift preferences for foraging options differing in two attributes by the addition of a suitably designed ADD [21,27,28]. For example, gray jays were offered choices between dishes containing different numbers of raisins placed at different distances into wire mesh tunnels. Preference is assumed to be an increasing function of the number of raisins, but a decreasing function of the distance that the jay has to venture into the tunnel. The birds increased their number of choices for the 'target' option (two raisins placed 56 cm into a tunnel) relative to the 'competitor' option (one raisin placed 28 cm into a tunnel) when an asymmetrically dominated 'decoy' option (two raisins placed 84 cm into a tunnel) was added to the choice set [28].

We believe that the most parsimonious explanation for this similarity in behaviour is that humans and animals use similar mechanisms when faced with complex multi-dimensional decisions, and that these mechanisms are based on comparative evaluation. However, further work is necessary to rule out other possible explanations for the observed effects of adding decoys, such as changes in state caused by alterations in rate of food intake [29].

Why might mate choice involve comparative evaluation?

There are several reasons why we might expect comparative evaluation of mates to have been favoured by natural selection as a mate choice mechanism:

(i) Females are often faced with a simultaneous choice between two or more males, making it possible for them to make comparisons among those males. This means that the number and range of males that a female has to choose between could influence her evaluation of potential mates. Simultaneous comparison of multiple males is likely to be particularly relevant in lekking species, in which males gather to display in close proximity to each other, and has been suggested as a specific advantage of leks [2].

(ii) Females typically vary in the number and type of males that they have previously encountered, and differences in past experience could therefore affect their evaluation of a given male [30,31].

(iii) Females are often faced with multi-component signals from males conveying a range of information. Just as in many human decision-making problems, the different kinds of information signalled by males are not necessarily positively correlated [11].

(iv) Females are likely to benefit from making mating decisions quickly and efficiently. Many studies have shown that there are fitness benefits from breeding earlier in the season, suggesting that there should be selection pressure for fast and efficient decision-making heuristics in females [32].

(v) From the perspective of the male, comparative mate evaluation could also have benefits. If females are using comparative evaluation mechanisms, then males can benefit by adjusting their level of signaling according to their competitors, because to be best a male only has to be just noticeably better than the other males with which he is being compared [33].

Thus, mate choice in animals appears to fulfil the criteria argued to have selected for comparative evaluation mechanisms in complex decision making in humans. We therefore propose that such mechanisms are also likely to have been selected for use in mating decisions. The crux of the comparative mate evaluation hypothesis is that the value that a female assigns to a male, and uses as a basis for her mating decisions, is not an absolute quantity directly reflecting the underlying quality of a male, but is instead a relative quantity that is dependent on the set of males that she has available for comparison. This choice set can comprise males that are simultaneously physically present, and memories of those previously encountered.

Evidence for comparative mate evaluation

Is there any evidence that comparative evaluation mechanisms are involved in mate choice? To answer this question, we need to consider what comparative mate evaluation predicts.

The most obvious prediction arising from comparative mate evaluation is that there should be variation in female preference depending on the social context in which she evaluates a male. This prediction emerges because the identity of the male that is judged as the best in a group of males will depend on the composition of the group. Consistent with this, there is considerable evidence that mating preferences vary both within and among individuals [34]. Although variation in female preference has not previously been attributed to comparative evaluation, this explanation needs to be explored. One particularly

attractive feature of the comparative evaluation hypothesis is that it provides a new explanation for why there is sometimes variation in the importance that females ascribe to different sexual signals in males with multicomponent displays [35,36]. This point is demonstrated by the human mate-choice experiment described in Box 2, in which females chose between males differing in the two attributes of physical attractiveness and sense of humour. The most physically attractive male, A, was chosen most often in the presence of the decoy male C_A, who had similar attractiveness to A but a poorer sense of humour. Whereas, by contrast, the male with the best sense of humour, B, was chosen most often in the presence of the decoy male C_B, who again had a similar attractiveness to B but a poorer sense of humour. Thus, whether attractiveness or sense of humour was more important to females was a function of the context in which they saw the same two males.

A particularly intriguing prediction to arise from the comparative mate evaluation hypothesis is that males could manipulate their attractiveness to females by selecting their social context appropriately. Returning to the human example in Box 2, male A can improve his ranking relative to male B by making sure that females see the pair of them in the presence of the decoy male C_A. Comparative mate evaluation therefore makes predictions about how males should position themselves spatially when displaying to females. Figure 2 makes this point using a well known visual illusion.

Finally, if females are using comparative evaluation mechanisms, then males should be selected to modulate flexible sexual signals, such as song, displays or extended phenotypes, depending on the other males with which they are being compared. Consistent with this, there is considerable evidence that social context can affect the sexual signals of a male [37,38].

In summary, although there is some evidence that is compatible with the comparative mate evaluation hypothesis, there are few in the way of conclusive tests, because although the above predictions arise from assuming comparative evaluation, they are not uniquely predicted by the hypothesis. Thus far, only one experiment has explicitly tested the effects on female preference of manipulating the presence of ADD males in a choice set. This study produced data that supported the ADD effect in human mate choice, and is described in Box 2 [17]. Analogous animal experiments that investigate the effects of modifying the size and composition of the male choice set on female preference are needed. If violations of regularity are found, these will constitute strong evidence for some form of comparative evaluation [18].

Summary and implications

Over a decade ago, Guilford and Dawkins [3] argued that researchers in behavioural ecology are perhaps too quick to jump to strategic explanations for observed behaviour. Although a tactical role for female perception in mate choice has been acknowledged for some time, we claim that a comprehensive understanding of female choice requires consideration of the cognitive mechanisms underlying decision making. We argue that the possibility of comparative evaluation offers a relevant contribution to such an understanding.

Of the many implications that follow from assuming comparative evaluation, we mention just two, one theoretical and the other logistical. The theoretical point is that comparative evaluation could offer a solution to the lek paradox by ensuring that the same male is not always chosen. We believe that this idea has considerable advantages over existing solutions based on errors in choice [39,40]. Rather than the variation in males being sustained by mistakes made by females, variation in choice by females using a comparative evaluation mechanism will occur whenever the context in which males are viewed changes. On a lek, it seems unlikely that males will be viewed in a standard context by all females, or, indeed, across time, even by the same female. Variation in female choice, then, need not be due to errors but rather to females 'seeing males in a different light'.

The logistical implication of assuming comparative evaluation is that results from choice experiments might need to be re-examined. In most experiments to date, the assumption is that females have an absolute view as to which is the preferred male, assuming that other aspects of context are constant [41]. If, however, the preference of a female is affected by the number and composition of the set of choice males, then at least some conclusions reached on the basis of such mate-choice testing might not hold under alternative testing conditions. It is possible, for example, that the inconsistent data from multiple laboratories from mate-choice tests on zebra finches (*Taeniopygia guttata*) could have arisen because female preference depends on the number and particular subset of males with whom she is presented, as well as her own past experience.

In conclusion, we believe that the comparative mate evaluation hypothesis offers rich material for future research in mate choice. The hypothesis suggests novel modelling opportunities and makes predictions that are open to experimental test. We hope that this brief review inspires researchers to consider the possibility of comparative evaluation mechanisms in mate choice, and design experiments to test some of the ideas that we have presented.

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