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Secondary sexual ornaments as signals: the handicap approach and three potential problems

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ABSTRACT. *Secondary sexual ornaments as signals: The handicap approach and three potential problems.*- Secondary sexual ornaments have recently been discussed in the context of biological signals, and the handicap principle has been suggested as a model explaining their evolution. The handicap principle predicts that at equilibrium, sexual ornaments will be honest signals of the male's quality. This is because the cost of ornaments to a potential cheater (a low quality male) will be greater than to an honest signaler (a high quality male), to an extent that makes cheating maladaptive. Accordingly, the cost of the ornament (the handicap) should be related to the quality it reveals. In the following, I discuss three problems with the handicap approach: i) It is difficult to determine the cost of the handicap and the quality it reveals. Nevertheless, I suggest that it is feasible and is worth doing. ii) It is not clear whether phylogenetic data can be used to distinguish between the handicap model and the sensory exploitation model. I suggest that it can be used only under restricted conditions. iii) Cheating (dishonest signalling) seems to contradict the handicap model. I will try to show, however, that some forms of cheating can be explained by the handicap model.

KEY WORDS. Sexual selection, Signlas, Handicap principle, Sensory exploitation, Cheating.

Introduction

The handicap principle (Zahavi, 1975; 1977; 1981; 1987) is a general model for the evolution of biological signals. Yet, it is most frequently discussed in the specific context of mate choice (Zahavi, 1975; Grafen, 1990a; Maynard Smith, 1991). According to the handicap principle, secondary sexual ornaments are extravagant signals developed by animals to attract the opposite sex, and like other signals, their evolution may be explained by the handicap mechanism. In the following, I shall discuss the handicap approach to the evolution of secondary sexual ornaments and deal with some related issues. I will first describe the handicap approach and the way I believe it should be used. I will then discuss three problems likely to be faced when trying to use the handicap approach. The first problem is how to determine the specific cost of a handicap and the quality it reveals, and how to determine that a certain cost really does function as a handicap. The second problem is whether phylogenetic data can be used to reject the handicap model and to support the sensory exploitation model instead. Finally, I will try to show how cheating (dishonest signalling) can be explained by the handicap model.

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The handicap principle: how it works

The reasons that brought many scientists to reject the handicap principle in its earlier days will not be discussed here (see Grafen, 1991, and Collins, 1993 for discussion on that subject). Recently, however, there is an increasing agreement among theoreticians that the handicap principle could work, and this has been demonstrated in several models (Nur & Hasson, 1984; Kodric-Brown & Brown, 1984; Pomiankowski, 1987; Hasson, 1989; Grafen, 1990a, 1990b; Pomiankowski et al., 1991; Iwasa et al., 1991; Maynard Smith, 1991; Godfray, 1991; Johnstone & Grafen, 1992; Schluter & Price, 1993). More important, these models present the handicap principle as the ESS solution for the evolution of signals, and predict that, at equilibrium, biological signals will be handicaps. In other words, according to these recent views, if we apply the optimization approach in studying animal communication, using ESS models and assuming evolutionary equilibrium, the stable outcome we are likely to get is the one predicted by the handicap principle (as suggested by Zahavi, 1977; 1981).

To explain the handicap principle in the evolution of male ornaments, the following scenario can be suggested: When males differ, genotypically or phenotypically, in their quality, females may benefit, directly or indirectly, from mating with high quality males. In this case, it will be advantageous for females to choose among males. If females choosing among males gather information on which to base their decision, then, all males should signal to females that they are of high quality. However, if all males are signalling that they are the best, females gain no relevant information and might do better by choosing at random. The conclusion is that female choice will be adaptive only when females base their decisions on reliable signals and ignore unreliable ones. It should be noted, however, that "reliable signals" do not have to be perfectly reliable (perfectly correlated with male quality), but only reliable enough (on the average) to benefit females who use them (i.e. to make the response to the signals better than a random choice). When females prefer reliable signals and ignore unreliable ones, males gain no benefit from using unreliable signals. Most males still benefit, however, from using reliable signals to show that they are still better than some other males. In conclusion, at equilibrium, both males and females are expected to use reliable signals. However, for all this to work, it is assumed that some signals are inherently more reliable than others. The missing part in this scenario is what makes some signals more reliable than others. The answer, provided by the handicap principle, is the cost of the signal.

The handicap principle predicts that, at equilibrium, sexual ornaments will be honest signals of the male's quality because the cost of the ornaments to a potential cheater (a low quality male) will be greater than to an honest signaler (a high quality male), to an extent that makes cheating maladaptive (Zahavi, 1987). A convenient example, illustrated by figure 1, is long tails grown by males of several bird species, apparently as secondary sexual ornaments (Jennions, 1993): If a long tail is costly, a tail of a given length imposes a greater cost on a low quality male than on a high quality male. Adding the benefit curve of a long tail due to mating success, shows that the optimal tail length for a high quality male is higher than for a low quality male (fig. 1). Tail length becomes an honest signal of the quality in consideration because if a low quality male tries to grow a tail which is longer than its individual optimum, his net benefit will decrease. In other words, the cost of the signal makes cheating maladaptive, and creates a correlation between tail length and male quality. It is important to note that this will be correct only if the quality in consideration is related to the cost of the tail. Otherwise, males of diffrent qualities would not differ in their ability to carry or to grow a tail.

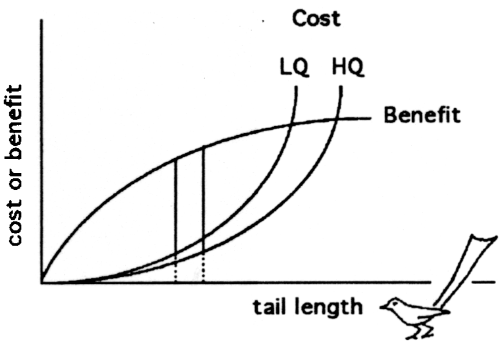


FIGURE 1. Optimal tail length for a low quality male (LQ) and for a high quality male (HQ) when a long tail is a handicap (see explanations in the text). Cost and benefit are measured using the same units of fitness (e.g. number of offspring). This allows to illustrate the handicap mechanism as in an additive model. It should be noted, however, that the actual functions creating the cost and the benefit curves might be multiplicative rather than additive (see, for example, Nur & Hasson, 1984).

[Longitud óptima de cola para un macho de baja calidad (LQ) y otro de alta (HQ) cuando una cola larga es un handicap.]

This condition creates the linkage between the cost of the handicap and the quality it reveals as suggested by Zahavi (1987).

The handicap approach and how to use it

As I have mentioned above, although the handicap principle is a unique model for the evolution of signals, it is an equilibrium model and is based on the optimization approach. Accepting this notion, might imply that similarly to the optimization approach (Maynard Smith, 1978), this principle should be used not only as a post-hoc explanation, but mainly as a model to pursue further research. For example, when studying clutch size in birds, behavioral ecologists do not argue that great tits lay an average clutch size of eight eggs simply because this is the optimal clutch size. Instead, they use optimization models (with a methodological assumption about equilibrium and optimality) in order to explore trade-offs and constraints that affect clutch size in birds. The question being asked in most of these studies is not whether clutch size is optimal, but why a certain clutch size might be more optimal than others. I believe that in the same way, the handicap principle should not be used only as an explanation for the existence of extravagant ornaments, but rather as a model to explore their meaning. Obviously, if we assume evolutionary equilibrium, any extravagant ornament used for communication may be a handicap. This is because the handicap mechanism is the equilibrium model for the evolution of signals. It would be interesting, of course, to know whether the ornament is indeed a handicap, as well as whether clutch size in birds is really optimal. However, using these models as a research program might be more productive than trying to prove that they are completely realistic (see Maynard Smith, 1978). The idea that an ornament is possibly a handicap, may lead to series of questions and hypotheses with testable predictions; If an ornament is a handicap, what type of handicap is it? What is the cost of this handicap? What is the quality it reveals? In other words, what is the message of the signal and why is it so important for females?

There are many possible costs for handicaps and many qualities they can reveal (Zahavi, 1987); For example, if elaborated ornaments handicap a male's ability to escape predation, the quality they reveal is that an ornamented male is relatively good in escaping predators. Ornaments that are energetically costly to carry may indicate that their owners are physically strong. Growing extravagant ornaments may be costly because it requires the investment of resources that could be used for other maintenance activities. In such a case, well developed ornaments indicate that their owners were in good condition at the time they grew them, and were able to recruit the needed resources. These kind of handicaps provide females with information on the male's history, which might be important if variations in male quality are mostly pronounced under the harsh environmental conditions that precede the breeding season. Another possible cost of ornaments is their vulnerability to parasites (Hamilton & Zuk, 1982). In such a case, ornamented male may advertise their relative resistance to parasites. The cost of having long ornaments may also be that they are more likely to be damaged during fights between males. If so, only good fighters can afford to grow long ornaments. The cost of a handicap need not be a very direct one. Ornaments or color pattern may not be costly by themselves but may clarify or amplify information about quality (Zahavi, 1979; 1987; Hasson, 1989; 1991). The cost of the ornament in this case is due to the information it provides. Low quality males may loose from showing their exact quality.

The examples above are probably not the only possible ones. With a little bit of imagination and with some understanding of the animal's biology, other good hypotheses can be generated. The first problem, however, is how to test these hypotheses.

Problem I: How to determine the cost of a handicap

The fact that some sexually selected ornaments appear to be condition dependent (Endler, 1980, 1983; Evans, 1991; Hill, 1991; 1992) suggests that they are indeed costly, because otherwise, males should grow them, or express them, under any circumstances. The problem, however, is that this evidence is only indirect, and not very specific as to what the exact cost might be. For example, Geoffery Hill (1991; 1992) showed that female house finches prefer to mate with brightly colored males. Male plumage brightness, in this case, is a function of a dietary intake and is correlated with male over winter survival and parental care activity. However, although it appears that ornamentation was correlated with the males' general quality, the specific cost which creates this correlation is not clear. Is it the cost of foraging for the required pigments, the cost of defending food resources that are rich in pigments, or the cost of expressing the pigment (that may increase predation risk, or amplify information about certain qualities).

An additional indirect evidence for the cost of secondary sexual ornaments comes from a recent comparative study (Promislow et al., 1992), which indicates that mortality cost may limit the evolution of male brightness in passerine birds. However, here again the specific cost of brightness that eventually affects mortality is unknown.

To test the specific cost of a handicap directly, an experimental manipulation is required. In numerous studies male ornaments were manipulated to test for female preferences. However, in only a few of these has the cost of such a manipulation been measured. Møller (1989) has shown that male barn swallows with experimentally elongated tail ornaments captured smaller, less profitable prey than those with shortened tails, and were more likely to have fault bars in their feathers (an indication of food deficiency during molt). Evans and his colleagues went even one step further. In a first experiment Evans & Hatchwell (1992) showed that the long tail of a male scarlet-tufted malachite sunbird handicaps its ability to fly and its efficiency at catching aerial insects. To test the cost of the handicap even more specifically, a second experiment was conducted. By adding extra mass on legs of some males and manipulating tail length of others, Evans & Thomas (1992) were able to show that the aerodynamic effect of a long tail, not its extra mass, is the cost of the handicap.

Elegant experiments of this type demonstrate that the specific cost of a handicap can be tracked. But, do they really show that the observed cost is the one that functions as a handicap (the one which create the correlation between the ornament and the quality)? To confirm that this is the case, one has to show quantitatively that the observed cost is high enough to make cheating maladaptive. To explain this point, let us imagine a case, illustrated by figure 2, in which carrying a long tail has been found to be energetically costly, and, as expected, this cost is relatively high for low quality males. However, when comparing the energetic cost to the benefit gained by mating success, it is found that the observed tail lengths in the natural population fall far below the optimal tail length predicted under the assumption that the cost of the tail is energetic. The conclusion in such a case is that energetic cost alone cannot account for the honesty of the signal, and additional costs should be searched for. The general conclusion here is that although a cost of any type is likely to be higher for low quality individuals, it can be regarded as a handicap only if it is high enough to limit ornament size.

A major difficulty when attempting to determine the cost of a handicap is to resolve cases in which no apparent cost is found. The problem with such negative results is that it is virtually impossible to prove that there is no cost (i.e. to prove that something does not exist). One can always argue that the researchers have simply failed to find the right cost, but perhaps one will be found in the future. If so, is there any way to reject the handicap model and to support an alternative explanation instead?

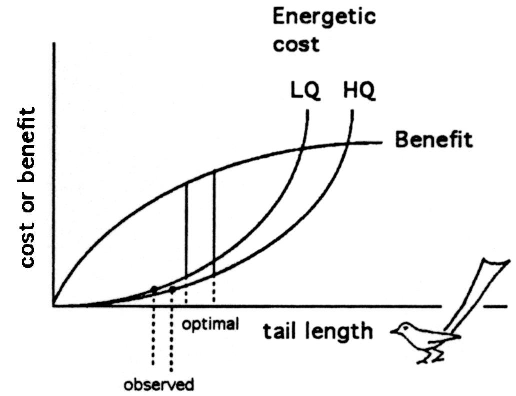


FIGURE 2. Expected optimal tail length of low quality (LQ) and high quality (HQ) males, based on the assumption that the cost of the tail is energetic, in relation to the observed tail length of these males in nature. The hypothetical case illustrated here suggests that energetic cost alone cannot account for the honesty of long tails as a signal. To simplify the illustration, the energetic cost, and the benefit of a tail are transelated into the same units of fitness (e.g. number of offspring), allowing to present the case as in an additive model (see comment in legend to Fig. 1).

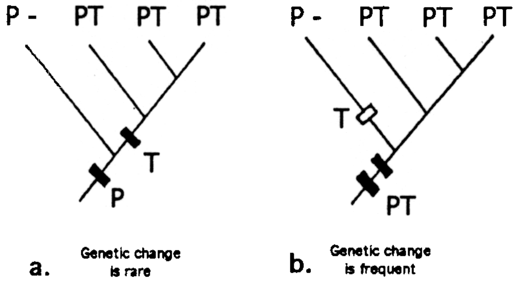
[Longitud óptima de cola esperada para machos de baja (LQ) y alta (HQ) calidad, basado en la premisa de que el costo de la cola es energético, en relación a la longitud de la cola de esos machos observada en la naturaleza.]

Problem II: Can phylogenetic data be used to reject the handicap principle and to support the sensory exploitation model instead?

Basolo (1990) and Ryan et al. (1990) have suggested that in some cases the evolution of female preference preceded the evolution of the male trait (ornament), and that the male trait has evolved to exploit this pre-existing preference of females. This model is commonly known as the "sensory exploitation model", although pre-existing preferences may not necessarily be based on sensory biases (A. Basolo personal communication). According to the sensory exploitation model, male ornaments may not be a handicap and may carry no message about a male quality. The ornaments evolved simply because females preferred ornamented males regardless of their quality.

There are two aspects to the sensory exploitation model. The first is the model itself, and the second is the use of phylogeny to test it (Basolo, 1990; Ryan et al., 1990; Ryan & Keddy-Hector, 1992).

The model itself is a good alternative scenario for the evolution of male ornaments. The difficulties arise when trying to distinguish between the alternative models. The first problem, as pointed out by Balmford and Read (1991), is that a trait that first evolved to exploit a pre-existing preference may be exaggerated later on, become costly, and turn into a handicap (see also Basolo, 1990; Ryan et al., 1990). Accordingly, even if we accept that in the past the trait was not a handicap, we cannot exclude the possibility that it does function as a handicap at the present. The second problem, which I discuss below, is whether the use of phylogeny can really distinguish between the alternative models.



a. Genetic change is rare

b. Genetic change is frequent

FIGURE 3. Alternative models to explain a phylogeny in which females of the least derived species have a preference "P" for a male trait "T" which occurs only in the more derived species. a) Assuming that genetic change is rare (i.e. parsimony), the preference evolved before the trait. b) Assuming that genetic change is frequent, the preference and the trait may have coevolved but the trait has subsequently been lost, probably due to selection (see explanations in the text).

[Modelos alternativos para explicar una filogenia en la que las hembras de las especies menos derivadas tienen una preferencia "P" por una rasgo de macho "T" que ocurre solamente en las especies mas derivadas.]

Using reconstructed phylogeny and experiments on female behavior, Basolo (1990) and Ryan et al. (1990) showed two clades (one of fish and a second of frogs) in which females of the least derived species prefer a male trait which occurs in the more derived species but not in their own species (see fig. 3). They suggested that the most parsimonious explanation for such a phylogeny is that the preference evolved before the trait (fig. 3a). Based on parsimony, the alternative possibility, that the trait and the preference coevolved together but that the trait has been lost, should be rejected because it requires more genetic changes (fig. 3b). There is evidence, however, that in some cases male ornaments have been lost while female retained their preference (McPhail, 1969; Basolo, 1991; Hill in press.). This might be expected if the trait was a handicap and became too costly under some circumstances (Schluter & Price, 1993; Hill in press). Accordingly, the alternative scenario (Fig. 3b) is possible, but it is only less parsimonious. The use of parsimony is therefore the sole criterion to prefer one model over the other.

Although the concept of parsimony is widely accepted, inadequate use of parsimony may lead to unrealistic conclusions. For example, based on parsimony, one can argue that a 20 year old car can still run properly because it has never broken down. It is quite obvious, however, that the alternative, and less parsimonious scenario, is more likely to be the correct one. Many break downs have probably occurred during the years, but the car has been fixed. Using parsimony in this case is improper because the concept of parsimony (Felsenstein, 1983) assumes that changes in the system are rare, while in fact, we know that many "changes" are expected to occur in a car within a period of 20 years. In conclusion, the critical information required to distinguish between the two alternatives is the frequency of changes. Because the concept of parsimony assumes already that this rate is low, it is not an independent criterion that can test which of the alternatives is correct.

Let us return now to sexual selection and the two alternative models illustrated by figure 3. If we assume that the genetic change (the mutation) required for creating a male trait is very rare (fig.

3a.), then it is likely that it occurred only once, and that the males of the least derived species are experiencing a long evolutionary lag: the trait is potentially adaptive (females prefer it) but it has not yet evolved. If, on the other hand, we have reasons to believe that these mutations are relatively common, then, it seems incongruent that during a long period of time this potentially adaptive mutation occurred frequently but never spread in the population. In this case the simplest explanation is that the trait is too costly for the males of that species, and was selected against (fig. 3b). In other words, the absence of male trait is adaptive and represents an equilibrium state. Similar to the example above, the critical information needed to distinguish between the alternatives is the frequency of changes. The concept of parsimony already assumes that this frequency is low, but this may not necessarily be the case.

In contrast with the concept of parsimony that minimizes the rate of genetic change (Felsenstein, 1983), optimization could occur only if there is sufficient genetic variance (Maynard Smith, 1978). Hence, these two legitimate approaches are based on opposite assumptions. Considering this, it is not surprising that parsimony supports the evolutionary lag scenario (fig. 3a) and rejects the equilibrium scenario (fig. 3b). The handicap model which is based on equilibrium, is therefore doomed to be rejected by parsimony under many circumstances. Parsimony cannot be used as an independent criterion to decide between equilibrium models and models that assume an evolutionary lag. It can only be used in cases where the rate of genetic change is known to be a limiting factor, and in such cases, equilibrium models are questionable anyhow.

It is important to note that the sensory exploitation model itself does not depend on a low rate of genetic change. Rather, it is the phylogenetic trees used to support the model that requires parsimony. I am not therefore arguing against the sensory exploitation model itself. I am, however, suggesting that the use of phylogeny to support it over the handicap model, should be based on some knowledge of the rate of genetic change, rather than on parsimony and its assumption of low rates.

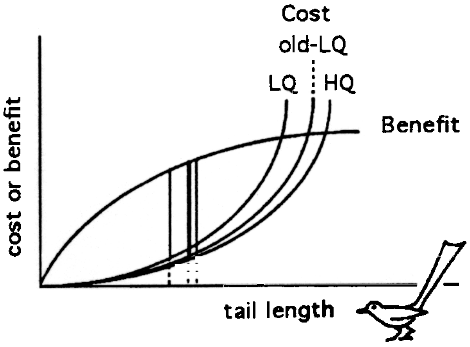


FIGURE 4. "Cheating" by an old male: If the cost of a given tail length decreases in old age, the optimal tail length for an old low quality male (Old LQ) may be higher than that of a low quality young male (LQ) and similar to that of a high quality young male (HQ). See text for more explanations. To simplify the illustration, cost and benefit are measured using the same units of fitness (e.g. number of offspring), allowing to present the case as in an additive model (see comment in the legend to fig. 1).

["Trampa" de un macho viejo: si el costo de una longitud dada de cola decrece al aumentar la edad, la longitud óptima para un macho viejo de mala calidad (Old LQ) puede ser superior a la de uno jóven de baja calidad (LQ) y similar a uno jóven de alta calidad (HQ).]

Problem III: How cheating can be explained by the handicap model

When explaining the handicap principle earlier in this paper, I emphasized that the cost of the handicap makes cheating maladaptive. If so, how can we explain evidence for cheating? In the following, I will try to show that according to the handicap principle cheating may evolve and may be stable, but only under certain circumstances. The concept is applicable for any signalling system based on handicaps, but will be discussed here only in the context of secondary sexual ornaments.

In cases where the male ornament is a long tail (fig. 1), cheats would grow tails longer than the average tail length of males of the same quality. In general, this will not be possible because all the males of a certain quality are affected by the same cost-benefit balance. Yet, cheating might be possible if there is an asymmetry in the cost-benefit balance imposed on different males of the same quality. A possible example for such a case has been recently suggested by Oren Hasson (in press) and I will further discuss it here.

It is assumed that one component of the cost of a long tail is reducing male probability to survive to the next breeding season. This component is less important for old males in their last breeding season (because in the suggested scenario the chances of old males surviving to the next year are very small). Hence, there is an asymmetry of costs between young and old males. In this case the optimal tail length of an old low quality male can be similar or even equal to that of a high quality young male (fig. 4). If females chose males based on tail length alone, a female that picked up an old male, chose a male of lower quality than the average quality of males with similar tail lengths. We can then argue that this female has been cheated. It should be noted that the average quality of males with a given tail length, and therefore the degree of cheating, is affected by the relative proportion of old and young males in the population. This kind of cheating will be stable if: a) It is too costly for females to discriminate between old and young males (if they can discriminate, cheaters will be selected against). b) Females still benefit on average from choosing males based on tail length, despite occasional cheating (otherwise they should not use the signal at all). c) Long tails are the best signal available to distinguish between males of different quality (If more reliable signals are available, females should use them instead).

The important conclusions from this example are that asymmetries in the cost of the handicap allow for some level of cheating in a system of handicaps, and that this asymmetry determines which individuals can be cheaters and which are honest signalers.

Conclusions

The handicap principle is suggested for use not only as an explanation for the evolution of secondary sexual ornaments, but mostly as a model to explore their meaning. Hypotheses regarding the specific cost of a handicap and the quality it reveals can be tested experimentally. However, a quantitative cost-benefit analysis is required to confirm that an observed cost really does function as a handicap. Using phylogeny to reject the handicap model and to support the sensory exploitation model, can be done only when there are reasons to believe that the rate of genetic change is low. In such a case, however, the handicap model that assumes equilibrium is questionable anyhow. Finally, even at equilibrium, asymmetries in the cost of the handicap between individuals of the same quality allow for some level of cheating in a system of handicaps.

Resumen

Ornamentos sexuales secundarios como señal: la aproximación del handicap y tres problemas potenciales.

Los ornamentos sexuales secundarios se han discutido recientemente en el contexto de señales biológicas, y se ha sugerido el principio del handicap como un modelo explicativo de su evolución. El principio del handicap predice que en el equilibrio, los ornamentos sexuales serán señales

honestas de la calidad del macho. Esto es debido a que el costo de los ornamentos para un tramposo potencial (un macho de baja calidad) será mayor que para un señalizador honesto (un macho de alta calidad), hasta el punto de que haga la tampa maladaptativa. De acuerdo con esto, el costo del ornamento (el handicap) debería estar relacionado con la calidad que manifiesta. Se discuten tres problemas con la aproximación del handicap: i) Es difícil determinar el costo del handicap y la calidad que revela. No obstante, se sugiere que es factible y merece la pena que se haga. ii) No está claro si los datos filogenéticos se pueden usar para distinguir entre los modelos del handicap y de la explotación sensorial. Se sugiere que sólo se puede hacer bajo condiciones restrictivas. iii) La trampa (señalización deshonesta) parece contradecir el modelo del handicap. Se tratará de mostrar, sin embargo, que algunas formas de engaño pueden ser explicadas por el modelo del handicap.

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