How to escape male infanticide: mechanisms for avoiding or terminating pregnancy in mammals

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ABSTRACT

The phenomenon whereby pregnancy may be inhibited or terminated when a female is exposed to non-sire males after mating is often, and rather generally, referred to as the ‘Bruce effect’. Widespread and indiscriminate use of the term for any case of pregnancy failure following exposure to an unfamiliar male, however, masks distinct physiological and social causes of the blocking or termination of pregnancy. Within the available literature, we identify four basic processes by which mammalian females can terminate pregnancy, and thus minimise risks of wasted reproductive costs which might result from male infanticide by a subsequent consort of any progeny carried to full-term where he was not the father. Physical contact with a non-sire male may induce pregnancy failure either before implantation (pregnancy block) or after implantation (pregnancy disruption). By direct contrast, in other species, physical presence of a familiar non-sire male may act to prevent the blocking or disruption of pregnancy, while separation from this non-sire male may act to trigger termination. We propose that use of the term ‘Bruce effect’ should be restricted to situations in which pregnancy failure is induced primarily by physical contact and/or odour stimuli from a non-sire male as in its initial formulation. Blanket use of this single term for all situations of pregnancy block or disruption, implying by default that pregnancy failure is the consequence of pre-implantation pregnancy block of an inseminated female as a result of physical contact with an unfamiliar male or his olfactory cues, masks the fact that, in many circumstances or species, very different mechanisms may operate in the prevention or disruption of pregnancy. The implicit presumption that pregnancy failure is a single and uniform phenomenon also discourages further research into the range of rather different circumstances and mechanisms by which pregnancy disruption may be triggered.
INTRODUCTION

The phenomenon whereby pregnancy may be inhibited (before implantation of the blastocyst) or terminated (after the blastocyst implantation) when a female is exposed to non-sire males after mating is often, and rather generally, referred to as the ‘Bruce effect’. Widespread and indiscriminate use of this term to refer to any case of pregnancy failure following exposure to an unfamiliar male has, however, tended to hinder recognition that in practice, the blocking or termination of pregnancy in such situations may be due to a variety of quite distinct physiological and social effects.

Hilda M. Bruce demonstrated clearly a failure of pregnancy and subsequent return to oestrus in laboratory mice Mus (Mus) musculus after exposure to a non-sire male or his urinary scent within a limited time after mating (Bruce 1959, Bruce & Parrott 1960, Bruce & Parkes 1961, Bruce 1963, Table 1). In these studies, Bruce established that pregnancy was blocked through direct inhibition of implantation of any fertilised egg(s). In this context and throughout the rest of the paper, ‘implantation’ is used to refer to the process whereby a fertilised egg becomes implanted in the lining of the uterus of placental mammals, a process also called nidation of the blastocyst (Shelesnyak 1960).

Table 1. Variations in understanding of the term ‘Bruce effect’

| Meaning of the term ‘Bruce effect’                                                                 | References                                                                                   |
|-------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|
| A pregnancy block and return to oestrus after the exposure of a female to an unfamiliar male or his urine within a limited time after mating (before fertilised ova implanted) | Parkes and Bruce (1961), Eleftheriou et al. (1962), Bruce (1965, 1970), Clulow and Langford (1971), Cheal and Sprott (1971), Kumar and Dominic (1993), Rülicke et al. (2006), Drickamer (2007), Wersinger et al. (2008), Becker and Hurst (2009), Pillay and Kinahan (2009), Guzzo et al. (2010), DeCatanzaro (2011), Guzzo et al. (2012), Marashi and Rülicke (2012), Ochiogu et al. (2012), and Thorpe and deCatanzaro (2012) |
| Inhibition of pregnancy by a ‘strange’ male before implantation, no mention of a specific role of olfaction | Clulow and Clarke (1968), and Kenney et al. (1977)                                                                                              |
| Any pregnancy termination resulting from replacement of the sire with an unfamiliar male       | Schwagmeyer (1979), DeCatanzaro and MacNiven (1992), Coopersmith and Lenington (1998), Ebensperger (1998), Blumstein (2000), Roberts et al. (2012), Gale et al. (2013), Eccard et al. (2017), Stokes & Sandel (2019), and Zipple et al. (2019a) |
| A general meaning of ‘pregnancy blocking’ or ‘pregnancy interruption’ in any context (although context correctly defined) | Labov (1981b), Heske and Nelson (1984), Labov et al. (1985), Thompson et al. (2007), and Zipple et al. (2019b) |
| Environmental threats to the survival of young; proximate conspecifics appear to induce spontaneous abortion in gravid females, both under laboratory conditions and in the wild | Catalano et al. (2016)                                                                                                                               |
| A ‘Bruce effect’ in humans implies that fewer high-need infants will be born when the environment increases morbidity and mortality among children | Catalano et al. (2016), Saxton et al. (2017), and Catalano et al. (2018)                                                                            |
| No usage of the term for post-implantation pregnancy disruption following exposure to a strange male, for example, “...predecessor’s offspring can be killed ... before birth either by preventing implantation (as with the Bruce effect) or by causing them to be aborted” (Bertram 1975) | Bertram (1975), Rosser and Keverne (1985), Kaba et al. (1989), McGuire et al. (1992), Bartoš et al. (2011, 2015, 2016) |

This phenomenon was popularly dubbed the ‘Bruce effect’ and generally regarded as a mechanism adopted by females to reduce the risk of infanticide by non-sire males of any offspring produced from the earlier mating (Schwagmeyer 1979, Ebensperger 1998, Blumstein 2000, Palombit 2015). In fact, the term ‘Bruce effect’ was used by Bruce herself in an article published in Science with her co-author A. S. Parkes (Parkes & Bruce 1961) and repeatedly thereafter, always with the meaning of implantation (pregnancy) block (Bruce 1965, 1970), later with emphasis on the olfactory cues in preventing implantation (Bruce 1970).

While it is widely regarded as a counterstrategy against infanticide, there are other possible explanations for this block or disruption of pregnancy. Bruce effects may have evolved as a mechanism of female choice (Schwagmeyer 1979); females that can prevent implantation and return to oestrus have, through such mechanisms, additional potential to select successful sires based on genetic fitness and thus ultimately maximise offspring fitness (Labov 1981a, Blumstein 2000, Rollo et al. 2014). In their natural state, house mice are largely territorial. In this case, contact with a non-sire male, or his odour cues, would suggest that the previous resident male has been displaced and thus that the new male is in some way superior or dominant or fitter. Among socially living animals, there are
also various benefits of mating with dominant males (Blumstein 2000), which may include minimising the risks of male infanticide (Horne & Ylönen 1996, Agrell et al. 1998).

Once it was described, many authors used the term ‘Bruce effect’ in the same context of pregnancy failure observed following exposure to stimuli from a non-sire male. Some continue to restrict the term to its original application (failure of implantation following exposure of a mated female to a different, non-sire, male, or olfactory cues from his urine). However, others have subsequently extended use of the term to other situations such as “any pregnancy termination resulting from the replacement of an original male by another adult male” or even, in a much more general way, to refer to any situation of ‘pregnancy blocking’ or ‘pregnancy interruption’. We have summarised some of the variation in the use of the term in Table 1.

Such casual use of the term has led to confusion and has masked some of the diversity of responses of mated female mammals to exposure to visual or olfactory stimuli from a non-sire male. Thus, for example, Mahady and Wolff (2002) noted: “The Bruce effect is a form of pregnancy disruption in mammals in which exposure of a female to an unknown male results in pre- or post-implantation failure (Bruce 1960)” . However, Bruce (1960) did not describe post-implantation male-induced pregnancy failure in her paper. On the contrary, she emphasised repeatedly that “pregnancy is protected only after implantation” (Bruce 1970). In the domestic horse Equus caballus, Bartoš et al. (2011) described that the proximity of a male who was not the father of the foetus increased the probability of post-implantation pregnancy disruption in mares; despite the fact that the effect described is clearly post-implantation, this study has been referred to as “additional evidence for the Bruce effect” by a number of subsequent authors (Roberts et al. 2012, Gale et al. 2013, Wang & Liu 2013, Rajabi et al. 2014, Zipple et al. 2017).

A few authors have discussed different concepts and mechanisms when introducing how they will use or interpret the term (Wolff 2003, Eccard et al. 2017, Stokes & Sandel 2019, Zipple et al. 2019a), but it is clear that in many other studies the term ‘Bruce effect’ is used somewhat indiscriminately without an exact definition or, if a definition is offered, with interpretation varying widely. Zipple et al. (2019b) argue that “the restriction of the term ‘Bruce Effect’ [to the specific case of pregnancy block] limits the utility of the term, since it could only be used when researchers had complete knowledge of the mechanism, and it would necessitate a different term for each mechanism involved, resulting in a proliferation of terms for phenomena that have the same functional significance”. We disagree with this view, arguing that scientists should seek precision in definitions wherever possible.

In this perspective, we aim to clarify terminology and consequences of the various different circumstances and conditions so far described which may lead to pregnancy block or disruption (listed, for example, by Eccard et al. 2017, Zipple et al. 2019a, b). The risk of infanticide and the physiological process involved in blocking or disrupting pregnancy are likely to be species-specific mechanisms, varying depending on ontogeny, and evolutionary history. The proximate factors are external stimuli, chemical, or social (presence or absence of sire; absence of a familiar male; presence of, or signals from, a novel, non-sire male; presence of another female or females; etc.) Whether or not such a mechanism is triggered in any circumstances is also likely to vary between species and will depend on the likely implications of association with the newly arrived non-sire male. We propose a formal classification of the process into four distinct categories of pregnancy failure, according to the timing when it occurs (before or after implantation of the embryo) and on positive or negative response to the presence of a non-sire male (Fig. 1). We hope that this formal redefinition of terms and mechanisms will help prevent some of the confusion (and problems of interpretation of new studies) that may arise from current terminological ambiguity. We emphasise that there are a number of different social and physiological mechanisms which may result in pregnancy termination in association with the presence of a non-sire male, and that therefore, different strategies and counterstrategies have evolved based on them.

Thus, for example, while there have been considerable advances in discovering the mechanism of pregnancy blocking in the house mouse (DeCatanzaro et al. 2001, Beaton & deCatanzaro 2004, 2005, DeCatanzaro et al. 2006, Becker & Hurst 2009, DeCatanzaro 2010, 2011, Guzzo et al. 2012, DeCatanzaro 2015; see also the extensive review by Zipple et al. 2019b), the same mechanisms cannot explain pre-implantation pregnancy block in the domestic dog Canis lupus familiaris (Bartoš et al. 2016) or the post-implantation pregnancy disruption described in the domestic horse (Bartoš et al. 2019) and domestic dog (Bartoš et al. 2016). When female dogs and horses were permitted close physical contact with non-sire males, the probability of maintaining pregnancy was higher than in females in visual or auditory contact with such males but prevented from direct physical contact.

**PRE-IMPLANTATION PREGNANCY BLOCK**

Pregnancy block through prevention of implantation of the blastocyst can be induced in a recently mated female house mouse by direct physical contact with an unfamiliar male mouse (Bruce 1959, DeCatanzaro et al. 1995b), but also by exposure to the priming pheromones of an
Fig. 1. Conditions under which mammalian females can block or terminate pregnancy either before implantation (pregnancy block: a, c) or after implantation (pregnancy disruption: b, d), triggered either by physical contact with a non-sire male (caused by semiochemicals in urine: a, b), or by separation from a non-sire male (preventing the mated female from mating with a non-sire male: c, d). *Male-induced pregnancy failure documented before as well as after the implantation. **Post-implantation pregnancy disruption triggered by separation from a potentially infanticidal male was proven in part of the data. References: 1: Bruce 1959, 1960, Parkes & Bruce 1961, 1962, Bruce 1963, Dominic 1964, Chipman & Fox 1966a, 1966b, Chipman et al. 1966, Bellringer et al. 1980; 2: Eleftheriou et al. 1962; 3: Mallory & Brooks 1980; 4: Clulow & Clarke 1968, Milligan 1976; 5: Stehn & Richmond 1975; 6: Clulow & Langford 1971, Mallory & Clulow 1977; 7: Clarke & Clulow 1973, Eccard et al. 2017; 8: Pillay & Kinahan 2009; 9: Marashi & Rülicke 2012; 10: Stehn & Richmond 1975, Kenney et al. 1977, Stehn & Jannett 1981; 11: Kenney et al. 1977; 12: Kenney et al. 1977; 13: Stehn & Jannett 1981; 14: Schadler 1981, Stehn & Jannett 1981; 15: Pereira 1983; 16: Mori & Dunbar 1985, Fashing et al. 2009, Roberts et al. 2012; 17: Sommer 1987, Agoramooorthy et al. 1988; 18: Colmenares & Gomendio 1988; 19: Pluhaček & Bartoš 2000, 2005; 20: Bartoš et al. 2016; 21: Berger 1983, Bartoš et al. 2011, 2015. [Colour figure can be viewed at wileyonlinelibrary.com]
unfamiliar male (Parkes & Bruce 1961, Dominic 1964, Chipman & Fox 1966a), major histocompatibility complex peptides from an unfamiliar male (Thompson et al. 2007), or oestrogens excreted in the urine of an unfamiliar male (DeCatanzaro et al. 2001, 2006, DeCatanzaro 2011, Guzzo et al. 2012, DeCatanzaro 2015). Pregnancy block is triggered by semiochemicals registered within the vomeronasal organ following nasal contact with male scent. This activates a specific vomeronasal neuroendocrine pathway that inhibits prolactin release, causing luteolysis (i.e. the structural and functional degradation of the corpus luteum) and is essential for establishing and maintaining pregnancy) and thus pregnancy failure and return to oestrus (DeCatanzaro & MacNiven 1992, DeCatanzaro et al. 1996, Becker & Hurst 2009, DeCatanzaro 2015).

Pre-implantation pregnancy block has been documented not only in the house mouse, but also in various other rodents (Fig. 1a). The domestic dog is the only species, so far, in which physical contact with a non-sire male before implantation was shown to result in a decrease in frequency of pregnancy failure rather than an increase (Fig. 1c). Females mated away from home but subsequently returned to a home pack containing a home non-sire male were shown to be eight times more likely to maintain pregnancy than females that were housed individually, but within sight of a home non-sire male or males, after their return home (Bartoš et al. 2016). In this case, it is presumed that the decreased pregnancy failure is because, if females were re-united with the home male, they could confuse him about paternity of the offspring by consorting with him and even copulating with him. Females who returned but were kept separated from the home male could not confuse paternity in the same way (Bartoš et al. 2016).

In house mice, pregnancy block only occurs during early pregnancy (pre-implantation), although it has been reported that female mice exposed to a novel male’s scent in late pregnancy weaned smaller offspring, probably by altering prolactin release, causing luteolysis (i.e. the structural and functional degradation of the corpus luteum) and is essential for establishing and maintaining pregnancy) and thus pregnancy failure and return to oestrus (DeCatanzaro & MacNiven 1992, DeCatanzaro et al. 1996, Becker & Hurst 2009, DeCatanzaro 2015).

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Thus, at least two alternative mechanisms can lead to pre-implantation pregnancy block. In one (Fig. 1a), the mated female has to come into physical contact with a non-sire male and/or his urine. This mechanism would ensure termination of existing pregnancies if a non-sire male entered the social environment (which, in most natural circumstances, would result from overthrow of the previous dominant or territorial male). In contrast to this (Fig. 1c), at least in the domestic dog, a female, who has mated away from the home environment, subsequently has to be in physical contact with the normal home (but non-sire) male in order to maintain pregnancy; termination rates are far higher in females who are not re-united with the home male. Females of many mammalian species do undertake mating excursions away from the home group. In species with a strong social structure and a strong possibility of infanticide by the dominant male of juveniles not of his siring, a female who has mated away from the group but subsequently has full access to the home male may be able to confuse him about paternity, reducing risks of subsequent infanticide. Females not in a position to confuse the home male about paternity might terminate pregnancies rather than risk the chance of later infanticide.

**POST-IMPLANTATION PREGNANCY DISRUPTION**

Post-implantation disruption of pregnancy (i.e. the resorption of the embryo or the abortion of the foetus) has been reported in voles, plains zebra *Equus burchelli* (now *Equus quagga*), domestic horse, domestic dog, and several primate species (Fig. 1b, d).

At least in the prairie deer mouse (Eleftheriou et al. 1962), domestic horse (Bartoš et al. 2011, 2015), and domestic dog (Bartoš et al. 2016) it is clear that post-implantation pregnancy disruption could not be purely due to pheromonal activity. The exact mechanism involved in post-implantation pregnancy disruption has not yet been fully explained, although it clearly involves active abortion or resorption of embryos. In feral domestic horses, Berger (1983) attributed several abortions following a change in the dominant male within a band to forced copulations by the new dominant male. He also mentioned a possible case of forced copulation in a plains zebra mare, leading to a termination of pregnancy in a zoo. However, from detailed observations of feral horses, Kirkpatrick and Turner (1991) came to contrasting conclusions. In their study, no incidents of harassment or attempts at forced copulation were witnessed, and seven of eight mares diagnosed pregnant produced foals. In studies on captive plains zebra, Pluháček and Bartoš (2000, 2005) did record four cases of possible abortion after forced copulation. Nevertheless, these copulations represented only 4.5% of nearly 90 possible cases when the mated female plains zebra was associated with a non-sire male (Pluháček & Bartoš 2000, 2005). Moreover, forced mating of pregnant females by...
a new male with no consequence on pregnancy was also observed (Pluháček & Bartoš 2005). Therefore, it does not seem likely that forced copulation would be a major factor inducing post-implantation pregnancy disruption, as argued by Zipple et al. (2019b).

Whatever the actual mechanism, pregnancy disruption may be triggered by stress associated with the presence of a new male, either when the female is in physical contact with him or his urine (DeCatanzaro & MacNiven 1992, DeCatanzaro et al. 1995b, Zipple et al. 2019b), or when she is not (Bartoš et al. 2011, 2016). Stress has been suggested in many studies to be a major factor triggering abortion in both non-human and human animals (Joachim et al. 2003, Nepomnaschy et al. 2007, Arck et al. 2008, Nakamura et al. 2008, Zipple et al. 2019b). Other factors, such as endogenous oestrogens or those excreted by males (DeCatanzaro et al. 1995a, 2001, 2006, DeCatanzaro 2010, 2011), may also be involved; other mechanisms may still be unresolved.

Actual physical contact with the non-sire male or, in some cases, his urine, is necessary to block early pregnancy in house mice and other rodents displaying the classic ‘Bruce effect’ (Bruce 1959, 1960, Bruce & Parkes 1961, Parkes & Bruce 1961, 1962, Bruce 1963, 1965, 1970, Jannett 1979, Drickamer 1989, DeCatanzaro et al. 1995a, van Schaik et al. 1999, Wersinger et al. 2008). Thus, females may maintain pregnancy simply by avoiding unfamiliar male scent during critical periods of susceptibility (Drickamer 1989, Becker & Hurst 2009).

At least in some species, such as the prairie deer mouse (Stehn & Richmond 1975, Kenney et al. 1977, Stehn & Jannett 1981), prairie vole (Kenney et al. 1977), meadow vole Microtus (Mynomes) pennsylvanicus (Kenney et al. 1977), montane vole Microtus (Mynomes) montanus (Stehn & Jannett 1981), pine vole Pitymys pinetorum, now Microtus (Pitymys) pinetorum (Schadler 1981, Stehn & Jannett 1981), several primate species (Pereira 1983, Mori & Dunbar 1985, Sommer 1987, Agoramooorthy et al. 1988, Fashing et al. 2009, Roberts et al. 2012), and plains zebra (Pluháček & Bartoš 2000, 2005), physical contact with a non-sire male is also essential to induce pregnancy disruption during the post-implantation period (Fig. 1b). In other cases, however, termination of pregnancy is more frequent if the female has visual contact with a familiar, but non-sire male while physical access is denied (Fig. 1d). Thus in the domestic horse (Bartoš et al., 2019) and in domestic dog females known to be pregnant (Bartoš et al. 2016), physical contact with the home male was actually needed to maintain pregnancy. In the domestic horse, pregnant females that were released into an enclosure with non-paternal males showed repeated sexual activity (Bartoš et al. 2011, 2015).

While this may sound like a special case, there is a body of evidence to suggest that other mammals may use the same strategy of mated females soliciting additional matings with non-sire, but socially significant, males. For example, Jeppsson (1986) found that female Eurasian water voles Arvicola terrestris (now Arvicola amphibius) that were already pregnant would mate with strange males they encountered while dispersing. The South African vlei rat Otomys irroratus may, in the wild state, be either polygynous or promiscuous; pregnancy termination after exposure to a strange male almost always occurred in polygynous females, but never occurred in promiscuous females (Pillay & Kinahan 2009). Even female house mice have been shown to move into neighbouring male territories to mate under semi-natural conditions (Potts et al. 1991).

Multiple-male mating and mating after conception have also been documented in many primates (Hrdy 1977, Hrdy & Whitten 1987, van Schaik et al. 1999), carnivores (Eaton 1978, Logan & Sweanor 2001), cetaceans (Connor et al. 1996, Clapham & Palsbøll 1997), rodents (Jeppsson 1986, Wolff & Dunlap 2002, Wolff et al. 2002, Pillay & Kinahan 2009), insectivores (van Noordwijk & van Schaik 2000), and ungulates (Asa et al. 1983, Hayes & Ginther 1989, Hooper et al. 1993, Crowell-Davis 2007, Bartoš et al. 2011). Thus multi-male mating may have evolved as a tool whereby females can confuse the dominant male (or males) within the normal social group about paternity, in order to minimise potential reproductive costs from infanticide (Hrdy 1977, 1979, van Noordwijk & van Schaik 2000, Drickamer 2007, Becker & Hurst 2009). Species with known post-conception mating are frequently also known to mate polyandrously before conception (Eagle et al. 1993, Kaseda & Khalil 1996, Agrell et al. 1998, Feh 1999, van Noordwijk & van Schaik 2000). Taking into account this high incidence, in a variety of mammalian species, of multiple-male matings pre- and post-conception, we suggest that pre-implantation pregnancy block and post-implantation pregnancy disruption may be much more common than has been documented. It is very likely that the lack of field evidence of post-conception mating and pregnancy block or disruption is due to lack of observations and the difficulty in detecting that block or disruption has occurred.

As in the pre-implantation pregnancy block, there are two spatio-temporal circumstances causing post-implantation pregnancy disruption. In one case, a mated female has to come into physical contact with a non-sire male to trigger pregnancy disruption (Fig. 1b). A different mechanism must be in effect when an away-mated female cannot get into physical contact with the normally present but non-sire male, in order to attempt to confuse paternity (Fig. 1d).
CONCLUSIONS AND FUTURE DIRECTIONS

Recognition of a distinction between the conditions under which pregnancy block and pregnancy disruption may occur is essential, because it should prompt further research into the bases of the different forms of block and disruption, and the strategies and counterstrategies of the species involved. While the presence of a non-sire male may block or disrupt pregnancy in some species, in other cases it may actually prevent pregnancy termination.

Male-induced pregnancy failure either before implantation (pregnancy block, Fig. 1a, c) or after implantation (pregnancy disruption, Fig. 1b, d), triggered by physical contact (Fig. 1a, b) or by physical separation (Fig. 1c, d) from a non-sire male whom the female may see, hear, or smell, each represent different situations by which mammalian females can terminate pregnancy and thus minimise reproductive costs due to male infanticide (Hrdy 1979, Schwagmeyer 1979, Labov 1981b, Ebensperger 1998, Drickamer 2007, Pillay & Kinahan 2009). Given the high incidence of multiple-male mating in various mammals, we suggest that post-implantation pregnancy disruption is a more common phenomenon than has so far been documented. Considering the strength of evolutionary selection on minimising reproductive costs, we suggest that promiscuous behaviour of pregnant females (documented by van Noordwijk & van Schaik 2000) may partly explain variation in mammalian mating systems.

In order to clarify terminology and assist further research, we propose that use of the term ‘Bruce effect’ should be restricted to those specific situations where exposure to a non-sire male or odour cues from such a male may act, in a previously mated female, to prevent implantation of the blastocyst. Blanket usage of this term, in all situations of pregnancy failure, by default implies that these are necessarily the consequence of pre-implantation pregnancy block of an inseminated female as a result of physical contact with an unfamiliar male or his urine, in place of a range of possible alternatives. Blocking of implantation (pre-implantation pregnancy block) induced by separation from a potentially infanticidal home male, and post-implantation pregnancy disruption induced primarily by mechanisms other than physical contact and odour stimuli should no longer be called the ‘Bruce effect’.

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