Highlights and Insights from “Biological Invasions and Animal Behaviour.”

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Abstract

Although behavior has long been considered central in understanding the causes and consequences of animal invasions, “Biological Invasions and Animal Behaviour” represents the first attempt to summarize the major advances in a single book. The book is a clear demonstration that behavior influences almost all facets of the invasion process. However, a common theme of the book is that general rules are rare. The role of behavior changes through the stages of the invasion process and within each stage can be highly context-dependent, implying that there may be several ways of being a successful invader. Despite the scarcity of general rules, there are two recurring generalization that emerge from the book. One is the central importance of behavioral plasticity in facilitating establishment and spread. The other is the appreciation that behavior is part of a suite of traits closely linked to life history, whose effects on population dynamics vary as a function of population size and degree of adaptive mismatch. Although aquatic ecologists have largely contributed to developing these ideas, their research has often been restricted to a few study systems and has mostly neglected mechanisms. Aquatic ecologists have, however, led research on the impact of invaders, using invasions as “unintended” experiments for examining the consequences of novel species interactions. This research unambiguously demonstrates that behavior is central to understanding how invaders alter native communities, notably by shaping predator–prey interactions. We believe that aquatic animals can continue providing research opportunities to further improve our understanding of the role of behavior in biological invasions, and we hope that “Biological Invasions and Animal Behaviour” may serve to encourage new research avenues.

Key words: behavioral syndromes, plasticity, learning, foraging, dispersal, boldness, predator/prey interactions

Behavior—the motor response to sensory information—has long been considered essential for understanding why some species succeed in new environments and what impacts they will have once established (Suarez and Cassey 2016). In the classic volume “Genetics of Colonizing Species,” Ernst Mayr (1965) highlighted the importance of behavior in defining the nature of successful invaders. For Mayr, behaviors such as the tendency to discover unoccupied habitats and the ability to shift habitat preferences were defining features of invasive species. Over 40 years later, researchers
have not only confirmed Mayr’s speculations on the central importance of behavior in invasions but have also found that the role of behavior is pervasive in almost all facets of biological invasions.

The role of behavior in animal invasions is more complex than previously thought, however. For example, we now know that the behaviors that help negotiate particular stages of the invasion process (Figure 1) may have little impact, or even be detrimental, at other stages (Chapple and Wong 2016). Our edited book “Biological Invasions and Animal Behaviour”, published in 2016 by Cambridge University Press, summarizes the major advances. It contains contributions from researchers throughout the world who study the role of behavior in the invasion process from a variety of perspectives, approaches and study systems.

Here, we summarize the most relevant contributions from the perspective of aquatic animals. Specifically, we discuss four major themes: 1) how the plastic nature of behavior assists individuals to thrive in novel environments, 2) how variation across individuals in less plastic behavior may also contribute to establishment by increasing the chances that some individuals are suitable to deal with the novel challenges and by facilitating evolutionary adjustments, 3) whether behavior should be considered as part of a life history syndrome to cope with environmental changes, and 4) how behavior helps predict the impact of biological invasions.

The importance of behavioral plasticity to thrive in novel environments

Novel environments confront animals with a wide variety of challenges, such as the need to adopt new foods or to avoid unfamiliar enemies. As behavior is an important way in which animals interact with their environment, the likelihood of establishment is expected to largely depend on the ability of individuals to adjust behavior to the new conditions. One way to do so is through decision-making. By choosing resources and habitats that better suit their phenotype, animals may enhance their fitness in novel environments (Sol and Maspons 2016; Sol et al. 2013). While aquatic ecologists have fundamentally contributed to our current understanding of the causes and consequences of such “Environmental matching choice”, the importance of this process in biological invasions has been under-appreciated. Instead, the importance of broad habitat and resource tolerances has attracted more interest, perhaps because many introduced animals are ecological generalists. In chapter 16, Tricarico and Acquiloni (2016) describe how alien crayfish occupy diverse habitats and tolerate a wide range of environmental conditions, features that are crucial for actively spreading to new habitats. Crayfish are omnivorous and opportunistic feeders, consuming a wide range of food items such as macrophytes, live macroinvertebrates, fish carrion, periphyton, detritus,
Figure 1. Stages of invasion and corresponding behavioural traits in the guppy. From Deacon and Magurran (2016) courtesy of Cambridge University Press.

molten conspecifics, small live fish and tadpoles (Gherardi 2007). The red swamp crayfish *Procambarus clarkii* (Girard, 1852) for example, feeds on the diverse items in an invaded habitat in proportion to their availability so that its diet can change with habitats.
Although environmental matching choice should generally improve fitness in novel environments, it may also lead animals to prefer to settle in poor-quality habitats if the choice reflects the expression of a prewired genetic program and the cues used to make decisions have changed in the new environment. The existence of such ecological traps has been documented in sea turtles. Their hatchlings rely on light cues from the open horizon to orient after emerging, but light pollution from beachfront structures may lead them to migrate inland instead of towards the ocean (Witherington 1997). The existence of ecological traps highlights that even though the expression of innate behavioral responses provides certain plasticity to cope with environmental changes, it may not be enough to cope with many of the challenges of novel environments. However, animals can respond to novel challenges in yet another way, through learning. In a novel environment, animals need to learn things such as which foods are edible and safe, which habitats are safe and appropriate for their needs, where good breeding sites are located or which species are predators and how to avoid them (Griffin et al. 2016; Sol and Maspons 2016; Sol et al. 2005). Crayfish quickly learn to feed on unknown prey: in the laboratory, naive individuals of Procambarus clarkii require less than 12 hrs to learn to maximize capture rate of unfamiliar larvae (Ramalho and Anastacio 2011).

Learning may thus facilitate establishment in novel environments by reducing environmental uncertainties and adaptive mismatches between the phenotype and the environment (Sol and Maspons 2016).

Once acquired, novel learned behaviors may be rapidly transmitted to other individuals through social learning (Griffin et al. 2016; Sol and Maspons 2016). Focusing on guppies, Poecilia reticulata, Deacon and Magurran (2016) show how behavioral flexibility resulting from both individual innovation and social learning contributes to the invasion success of this species (Figure 1). As an omnivore, the guppy has dietary flexibility and can capitalize on whatever food is available in a new habitat. They can learn to navigate a maze to reach food, and to consume novel foods (Laland and Reader 1999). Using social learning, an individual guppy can learn the route to a new food source by following conspecifics through a maze. This ability might be related to their evolutionary history in variable environments. In their native habitat, guppies repeatedly move from downstream sites with higher predation to upstream sites with lower predation, and then wash back down again. Deacon and Magurran (2016) argue that this exposure to conditions of naturally varying risk might have selected for the flexibility to cope with different environments and predator regimes.

Learning can also facilitate invaders acquiring knowledge from more experienced native species on key issues such as how to exploit or to avoid enemies (see Sol and Maspons 2016). In aquatic animals, the use of such
public information has been documented in the context of predator avoidance. The invasive *P. clarkii* decreases its risk of predation in new environments by quickly learning predator avoidance behaviors from heterospecifics. The species appears to be more sensitive to predator presence than native species, using a broader range of information about predation risk and reacting more strongly to heterospecific alarm cues that elicit the typical alarm reaction (i.e. stop movements to avoid being detected). Individuals of the invasive virile crayfish, *Orconectes virilis* respond similarly to alarm cues from conspecifics, sympatric heterospecifics and novel heterospecifics, suggesting that these animals use a wider range of information about their environment, and enter a new habitat with the ability to respond adaptively to a wide range of predators (Hazlett et al. 2002, 2003).

**The personality of successful invaders**

While the importance for invasions of behavioral plasticity is without doubt, the common view that successful invaders should be characterized by particular behavioral types is less clear. For example, the view that boldness and aggressiveness should be major features of successful invaders has proved difficult to demonstrate empirically, in part because the contexts in which they apply may not be so common (e.g. Sol et al. 2012). Still, the book presents convincing evidence that certain personality traits, i.e. behavioral traits that are consistent within individuals over time (Sih et al. 2004, 2012), are highly relevant in particular contexts (Chapple and Wong 2016). For example, a spreading population encounters novel conditions and dispersal barriers (e.g. obstacles, natural geographic and human-made features, unsuitable habitat) that must be overcome in order to be successful and become established in new areas. Behaviors that may be relevant to cope with these difficulties include dispersal tendencies, aggressiveness, boldness, activity, exploratory behavior and sociability. Rehage et al. (2016) draw from their studies on the mosquitofish, one of the 100 worst invasive species in the world, to discuss the importance of personality in spreading. Only some species of *Gambusia* are, in fact, invasive. The invasive ones exhibit greater exploratory tendency (Rehage and Sih 2004) and foraging efficiency but do not differ in boldness from their noninvasive congeners.

The existence of individual variation in behavioral types within a population can also be highly relevant to understand how animals negotiate the different stages of the invasion process, as this increases the likelihood that at least some individuals have the appropriate behavior to negotiate the sequential filters of the invasion process (Wong and Candolin 2015). In mosquitofish, among individual variation in aggressiveness and sociability has been related to range expansion of successfully established
populations. Sociability affects the tendency to form shoals (Cote et al. 2010) and is likely to reduce dispersal, while asocial, aggressive individuals are more likely to disperse (Figure 2). Thus, more aggressive and asocial individuals are more likely to invade new habitats and establish populations. While the existence of variation in behavior among individuals has been amply documented for aquatic animals, the general importance of this variation for the different stages of the invasion process is generally unknown due to the paucity of empirical evidence.

**Behavior as part of a life history syndrome**

It is increasingly appreciated that behavior should not be considered in isolation but as part of a broader complex of adaptive traits that mediate the response of individuals to new environments. Although the importance of behavioral syndromes is discussed in several chapters, Sol and Maspons (Chapter 5; see also Phillips 2016) extend the idea to consider behavioral responses as part of a pace-of-life history syndrome to cope with responses to environmental changes (Figure 3). In a context of environmental uncertainties and displacement from the adaptive optimum, theory predicts that a life-history strategy that gives priority to future rather than current reproduction either through a long reproductive life or reproducing several times in a same season should be particularly beneficial. Such a future returns strategy reduces the costs of a reproductive failure by spreading reproductive effort over many events (i.e. avoiding “putting all the eggs in a single basket,”) and by enabling delaying reproduction if conditions are unfavorable. These expectations from life history theory acquire even more relevance when considering the role of behavior. The ability to delay reproduction increases, for instance, the opportunities for acquiring environmental information and, through learning, improve behavioral performance in exploiting resources and avoiding enemies.
When the population is small, which is often initially the case for introduced species, and there is sufficient phenotype-environment match, a future returns strategy may not be the best solution. In such a scenario, it may pay to have a high fecundity that allows rapid population growth, thereby reducing the period at which the founder population remains small and hence more vulnerable to extinction by demographic stochasticity (Lockwood, 2009). In Chapter 17, Mark Albins examines the range of life-history and behavioral traits that have facilitated the rapid invasion of introduced lionfish (Pterois spp.) in the Atlantic. Lionfish, which were probably initially released from aquariums in South Florida, have become one of the worst fish predators, having major impacts on native coral reef fishes throughout the Caribbean, Gulf of Mexico, and South Atlantic. The rapid population growth and spread of invasive lionfish have been primarily attributed to their life history characterized by fast growth and maturation, and a high fecundity, fertilization success, and survival of eggs and larvae. It can also be attributed in part to the lack of dispersal barriers in the open water. Their population growth and spread have also been facilitated by behavioral mechanisms. The eggs and larvae are able to travel long distances, while after settlement, the fish tend to stay around the same area. While in their native range they tend to be solitary except during spawning periods, in the invasive range they are either more social or are continually ready to spawn. This finding contrasts with the previously discussed studies of Gambusia, where asocial individuals are more likely to invade new habitats and establish populations, illustrating the idiosyncrasies of the process.
Behavioral syndromes associated with life history can evolve in the novel environment if the underlying components are heritable and together provide fitness advantages in the new context. Surprisingly, however, there has been little research on eco-evolutionary dynamics of behavior in invading populations. The studies of cane toads (*Rhinella marina* Linnaeus, 1758), a species that is primarily terrestrial but that rely on water to lay the eggs, are an exception. Ben Phillips (2016) describes in Chapter 6 how eco-evolutionary dynamics changes the spreading rates of cane toads introduced in Australia. As only the most dispersive individuals get to the invasion front of the population in any given generation, there will be assortative mating by dispersal ability (Phillips et al. 2008, 2010). This spatial sorting causes the runaway evolution of the dispersal trait. In addition, individuals in the front of the expanding range find themselves in an exponentially growing population which, according to r/K theory, should select for higher fecundity. Conditions at the invasion front therefore favor the evolution of greater dispersal and reproductive rates, which should accelerate spreading rate over time. In cane toads, the rate of spread has indeed been accelerating since the original introduction and now is five times faster than the original rate.

### Behavioral interactions between invaders and native species

As highlighted by Suarez and Cassey (2016), invasions provide a powerful “unintended” experimental system for examining novel species interactions, including predator-prey and host-parasite co-evolution. Chapters in this section discuss a variety of interactions, including predator-prey, host-parasite, and mutualistic networks. In the chapters dealing with aquatic systems, however, there is an emphasis on predator–prey interactions. In Chapter 11, Weis (2016) examines freshwater and marine ecosystems, discussing the wide-ranging impacts of invasive predators on both native prey species specifically and invaded ecosystems generally. Among the highlighted crustaceans are green crabs (*Carcinus maenas* Linnaeus, 1758) which manage to outcompete many native species for bivalve prey (MacDonald et al. 2007), and rusty crayfish (*Orconectes rusticus* Girard, 1852) which also outcompete native crayfish in the US and are less affected by predation by largemouth bass (Hill and Lodge 1999). Among the fishes discussed are rainbow trout (*Oncorhynchus mykiss* Suckley, 1869) that have been introduced for food or sport fishing in many continents and have spread throughout the world. By feeding on native salmonids and other fish species as well as on amphibians and terrestrial insects, rainbow trout reduce the population of their prey and have complex effects on both aquatic and nearby terrestrial food webs (Fausch 2007).

Behavior is central to understand these novel interactions between predators and prey. In their chapter, Grosholz and Wells (2016) focus on
the role of predators in recognizing, selecting, handling and consuming novel prey, whether as native predators consuming novel prey, or as non-native predators consuming native prey. It is believed that introduced predators prefer familiar prey and would need time to become accustomed to novel prey, so there should be time lags before interacting with novel prey that should attenuate over time (Hastings et al. 2005). To explore these ideas, Grosholz and Wells (2016) examined introduced predatory whelks and their new oyster and mussel prey. Experiments with both native and introduced populations of oyster drills, *Urosalpinx cinera* (Say, 1822), showed that shared evolutionary history does not appear to be a major mechanism underlying choice of oysters or mussels as prey. The preferred oyster was either the familiar *Crassostrea virginica* (Gmelin, 1791) or the novel *Ostrea lurida* (Carpenter, 1864), depending on circumstances, whereas the preferred mussel was the novel *M. senhousia* (Benson, 1842). Naïve *U. cinerea* immediately preferred *M. senhousia* despite lack of any prior experience. For the population of *U. cinerea* from the introduced range, the lack of any experience with *C. virginica* for several decades did not reduce their preference for *C. virginica*. Thus, the choices made by this predator with novel vs. familiar prey do not seem to follow predictions. The authors concluded that if the cues used in these systems are general and not species specific, there may be little functional naïveté, and if the new prey species are similar to familiar species, the level of naïveté will be low and easily overcome by learning.

Behavioral responses of natives to the invaders are also important to consider. When the invader is a predator, native prey are generally naïve and more susceptible to predation, which contributes to the success and impact of the invader. This is particularly clear in the case of invasive lionfish (*Pterois volitans* Linnaeus, 1758) in the Atlantic and Caribbean, where they consume large numbers of juveniles of many coral reef fish species that are naïve and do not react to the predator, reducing their populations (Albins 2013, 2015). To make things worse, in their invaded range, lionfish consume far more food than in their native range and become larger (Fishelson 1997; Cote et al. 2013).

In some cases, the invader becomes a new food source for native species. Invasive Pacific oysters (*Magellanica gigas* Thunberg, 1793) develop reefs which become feeding areas for coastal birds in Europe (Herbert et al. 2018). In cases where the native predators are very abundant, they may be able to slow down or arrest the invasion. In the Chesapeake Bay, US, blue crabs (*Callinectes sapidus* Rathbun, 1896) are very abundant, and appear to provide some “biotic resistance” to the invasion of green crabs (*Carcinus maenas*), which are much more abundant in areas further north where there are fewer blue crabs (deRivera et al. 2005). Blue crab predation may similarly be responsible for reducing the numbers and impacts of the
invasive rapa whelk, *Rapana venosa* (Valenciennes, 1846), in Chesapeake Bay (Harding 2003). In some cases, the invasive species is toxic and can be a hazard to its potential predators. Venomous spines of lionfish can be a major deterrent to predation, and low predation rates enhance its success as an invader (Albins 2016). In other cases, toxic invaders can be consumed by naïve predators. Hatchlings of the toxic invasive toad, *Bufo japonicus formosus* (Temminck and Schelgel, 1838) in its invaded range are preyed upon by native amphibians, including carnivorous salamander larvae *Hynobius retardatus* (Dunn, 1923) and omnivorous frog tadpoles, *Rana pipica* (Matsui, 1991). In mesocosm studies, Kazila and Kishida (2019) found that both predator species were adversely affected by consuming toxic toad hatchlings, but that the frog tadpoles were more greatly affected because they had lower toxin resistance. Regarding toxic cane toads in Australia, mass mortality was seen in predatory crocodiles (*Crocodilus johnstoni* Krefft, 1873) coincident with the arrival of the toads, causing the crocodile populations to decrease by as much as 77% (Letnic et al. 2008). Some mammalian predators have apparently learned to refrain from attacking the toxic toads. While naïve individuals of the marsupial, *Planigale maculata* (Gould, 1851), would initially seize the toads, they rapidly learned to avoid them (Webb et al. 2008). However, another native marsupial, the northern quoll *Dasyuris hallucatus* (Gould, 1842) apparently did not learn to avoid cane toads and became locally extinct in Northern Australia following the invasion.

Native species may change their habitat or location in order to avoid predation or competition from the invasive species. In many cases, this relocation is detrimental. In response to the invasive predatory cladoceran, *Bythotrephes longimanus* (Leydig, 1860), *Daphnia galeata mendotae* (Birge, 1918) were found to move deeper into the water column in lakes to avoid the predators, but this resulted in a reduction in their growth rate (Pangle and Peacor 2006). Invading rainbow (*Oncorhynchus mykiss*) and brown (*Salmo trutta* Linnaeus, 1758) trout in Patagonia caused the native galaxiid fish, *Galaxias platei* (Steindachner, 1898), to similarly move down to feed at greater depths in the lakes, which was interpreted as a response to depletion of their prey in lakes that had high trout density (Correa et al. 2012). In response to the invasion of the benthic round goby (*Neogobius melanostomus* Pallas, 1814) in the US Great Lakes, juvenile smallmouth bass (*Micropterus dolomieu* Lacépède, 1802) were found to move up from the bottom to find food in the water column, which forces them to eat small plankton rather than larger benthic macroinvertebrates. This location in the water column also makes them more vulnerable to predators (Winslow 2010). Native sculpins, *Cottus beldingi* (Eigenmann and Eigenmann, 1891) in California streams live in pools and low velocity habitats. However, when invasive signal crayfish (*Pacifastacus leniusculus* Dana, 1852) arrive the sculpins move to more rapidly flowing water, where
they have reduced feeding and growth (Light 2005). Native Dungeness crabs (*Cancer [Metacarcinus] magister* Dana, 1852) in the Pacific coast of the US are displaced from their shelters by invasive green crabs (*Carcinus maenas*), enhancing their risk of predation (McDonald et al. 2001). However, native shore crabs, *Hemigrapsus oregonensis* (Dana, 1851), in turn, were able to displace the green crabs from their habitat of rock and shell cover (Jensen et al. 2001).

**Management implications**

Understanding the behavior of animals during the invasion process can offer management opportunities. Prevention is widely considered a more efficient way to reduce the impact of biological invasions than control and eradication. In chapter 18, Carrete and Tella (2016) discuss the role of behavior in preventing escapes from the pet trade, one of the major pathways of animal introductions. As behaviors related to anti-predator and foraging abilities may be eroded in captivity, in theory, animals that have been bred for the pet trade should be less likely to escape and establish breeding populations, thereby failing to complete the two main transition stages (release and establishment) of the invasion pathway. Some examples of successful invasions in aquatic pets, such as lionfish, show nonetheless that this is not always the case. Although bans may represent a successful management action against invasions, the relevance of behavior during the early stages of the invasion process is unfortunately poorly understood for aquatic animals because their presence tends to be discovered later in the invasion process.

A variety of management options that use behavioral information to control invaders are also discussed throughout the book, although their validity remains to be tested. The chapter on the spread of cane toads in Australia illustrates this (Phillips 2016). Because toads at the leading edge of the invasion are more dispersive, physical barriers such as rivers and mountains, that might have acted as barriers, are less effective. If individuals from long-established populations are moved to the invasion front, those physical barriers might remain effective and the highly dispersive phenotypes might never reach the barrier because the individuals moved to the invasion front are less dispersive and less likely to penetrate the barrier. Understanding hormone-behavior relationships in invaders may also reveal new ways to control pests; yet, it is rare that endocrinological interventions are used to stop or slow invasions (Martin et al. 2016). A final management option that is being considered for some invasive species is to add human predators to the top of the food web to consume the invasive species (Weis 2016). This is being pursued throughout the Caribbean and South Atlantic for the lionfish, *Pterois* spp.
Concluding Remarks

The chapters of the book reflect the current vitality of the discipline, illustrating the many ways behavior influences biological invasions. A common theme in these chapters is that general rules for predicting invasion success are rare. This may indicate that there is no single strategy to employ in order to be a successful invader, reflecting the variety of mechanisms by which behavior affects population dynamics in novel environments. It also indicates that the role of behavior often depends on the invasion context. The study of aquatic systems has been essential to unravel the idiosyncratic forms invaders may use to invade and impact ecosystems.

Arguing that general rules are rare is not to say that there are no rules. In fact, the book highlights a general consensus that behavioral plasticity is a key feature of many successful invaders. However, even in this case the context matters, and being plastic is less relevant under certain contexts, such as when demographic stochasticity is high and/or the species is only weakly displaced from their ancestral adaptive optimum. Understanding the contexts in which particular behaviors or behavioral mechanisms are beneficial is complicated by the fact that they are part of a suite of traits that influence the way animals negotiate the invasion process, from capture to spread. Making the link between behavioral syndromes and invasion contexts is crucial because at an ultimate level, these suites of traits are closely tied to evolving life history strategies that govern the population dynamics in novel environments. Therefore, the consequences of behavior for population dynamics cannot be simply inferred by examining behaviors in isolation. Again, aquatic systems have provided some of the best model systems (e.g. cane toads and guppies) to study the eco-evolutionary dynamics of behavioral syndromes during invasions.

Reading Biological Invasions and Animal Behaviour, however, it becomes clear that there are still important gaps in our knowledge about how behavior affects and is affected by biological invasions. Some of these gaps are general to the discipline. We have, for instance, an insufficient understanding of how behavioral plasticity interacts with life history to influence population dynamics in novel environments. In a similar vein, the importance of evolution in shaping behaviors is almost absent in the book, despite ample evidence that much among-individual variation in behaviour is heritable and that, by acting on such variation, natural selection can alter the invasion process itself (Phillips 2016). Other knowledge gaps are particularly important for aquatic animals. One is the hormonal basis of the behaviors that are relevant at different stages of the invasion process (see Martin and colleagues in Chapter 4). Martin and colleagues (2016) predict that successful invaders should be those species that are better able to up- and down-regulate circulating hormone levels to salient stimuli,
adjust hormone receptor expression among tissues, and/or couple and uncouple other processes (e.g., immune, growth, reproductive) to hormones. However, these ideas have been mostly developed for terrestrial animals, and it is currently unclear whether they should also apply to aquatic systems. Another topic poorly known for aquatic animals is the proximate cognitive basis of behavioural responses to new ecological challenges. This topic, which is widely discussed by Andrea Griffin and colleagues in Chapter 3 (Griffin et al. 2016), is better known for terrestrial invaders than for aquatic invaders. Finally, discussions on role of behaviour in the early stages of the invasion process are notoriously rare for aquatic animals. This is unexpected because some early stages where behavior should be highly relevant, such as escapes from the pet trade, are major pathways of introduction of aquatic organisms. By suggesting ideas, methods and study systems, we hope that “Biological Invasions and Animal Behaviour” serves to encourage aquatic ecologists to continue investigating how behavior allows animals to negotiate the wide range of hurdles animals encounter during the invasion of novel regions.

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