

5 Life History, Behaviour and Invasion Success

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At the most fundamental level, biological invasions hinge on the fate of individuals surviving and reproducing in novel environments. If individuals are able to reproduce at a higher rate than they die, the invader will increase in numbers and can eventually become established and spread; if the balance is negative, however, the population will decrease over time and end up extinct. Because the rates of birth and death are ultimately determined by how organisms allocate their limited time and energy to reproduction and survival (Stearns, 1992), life history theory has long been deemed essential to understanding the success of invaders (Lewontin, 1965).

Surprisingly, however, life history theory has achieved little success in predicting the outcome of organisms' introduction (Blackburn *et al.*, 2009; Sol *et al.*, 2012b). One problem is the excessive focus on the small population paradigm, implicitly assuming that demographic stochasticity is the main driver of extinction in introduced populations. This has led to the widespread belief that successful invaders are characterized by high fecundity that reduces the exposure to demographic stochasticity by enhancing population growth (Moulton *et al.*, 1986). Nevertheless, for an invader coming from a distant region, unfamiliarity and insufficient adaptation to the new resources, enemies and other hazards are also likely to increase the risk of extinction by negative population growth. Life history theory offers additional mechanisms that may help mitigate these effects, such as bet-hedging (Starrfelt and Kokko, 2012) and the storage effect (Warner and Chesson, 1985; Caceres, 1997). However, as we argue in this chapter, if we want to fully understand how life history affects animal invasions, we need to explicitly consider the role of behaviour.

Our argument for the need to better integrate behaviour into life history theory is founded upon three main principles. The first is the fact that behavioural responses are part of the adaptive machinery of animals to cope with uncertainties and evolutionary disequilibria of novel environments. While the idea is not new (Mayr, 1965), recent theoretical and empirical advances provide a strong foundation for moving forward. The second argument is the growing evidence that behaviour affects and is affected by life history, which implies that both are part of a same adaptive strategy. Thus, when we examine how life history affects invasion success we are considering not only life history mechanisms but also mechanisms related to behavioural responses to novel

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environments. The last argument is that behaviour mediates some life history mechanisms of response to novel environments, particularly those related to environmental uncertainty and adaptive mismatch. By clearly delineating these mechanisms, we can better infer when it is necessary to consider behaviour.

Altogether, the above principles create a new way to understand how life history influences population growth in novel environments, potentially contributing to a more predictive theory. Such a theory is necessary not only to better understand the invasion process, but also as a basis to help prevent and mitigate the ecological and economic impact of biological invasions (Kolar and Lodge, 2002; Vall-llosera and Sol, 2009; Leung *et al.*, 2012). Because invaders represent unique opportunities to evaluate how organisms cope with sudden environmental changes, the new theory should also be of great importance in predicting extinction risk associated with human-induced rapid environmental changes like habitat destruction and climate change (Sæther and Bakke, 2000; Sih *et al.*, 2011).

Life History Mechanisms Influencing Invasion Success

Before trying to integrate behaviour into life history theory, we will describe the variety of mechanisms by which life history can directly influence invasion success, highlighting the problems of classic theory and discussing mechanisms that extends the framework to scenarios beyond the small population paradigm.

Problems of Classic Theory

The debate regarding how suites of life history characteristics affect invasion success has been dominated by two opposed perspectives, both related to the so-called fast-slow continuum of life history variation (Figures 5.1 and 5.2). The most popular is the population growth hypothesis, proposed by Lewontin (1965) more than 45 years ago. This hypothesis predicts that successful invaders should be characterized by a fast-lived strategy in which fecundity is prioritized over survival (Figure 5.1); such a strategy allows rapid population growth, thereby reducing the period at which the founder population remains small and hence more vulnerable to extinction by demographic stochasticity (Moulton *et al.*, 1986; Figure 5.3). Demographic stochasticity arises because the discrete and probabilistic nature of the birth and death of each individual leads to random fluctuations in population size, which in a small population can largely increase the risk of accidental extinction.

The opposite view to the population growth perspective is the hypothesis of the life history buffer (Pimm, 1991; Saether *et al.*, 2004; Forcada *et al.*, 2008). This hypothesis argues that successful invaders should be characterized by slow-lived strategies because their populations are less prone to large stochastic population fluctuations that can accidentally result in extinction. The mechanism is again the discrete and probabilistic nature of the birth and death of individuals. Thus, although a slow-lived species will recover more slowly from a small population size than a fast-lived species, this

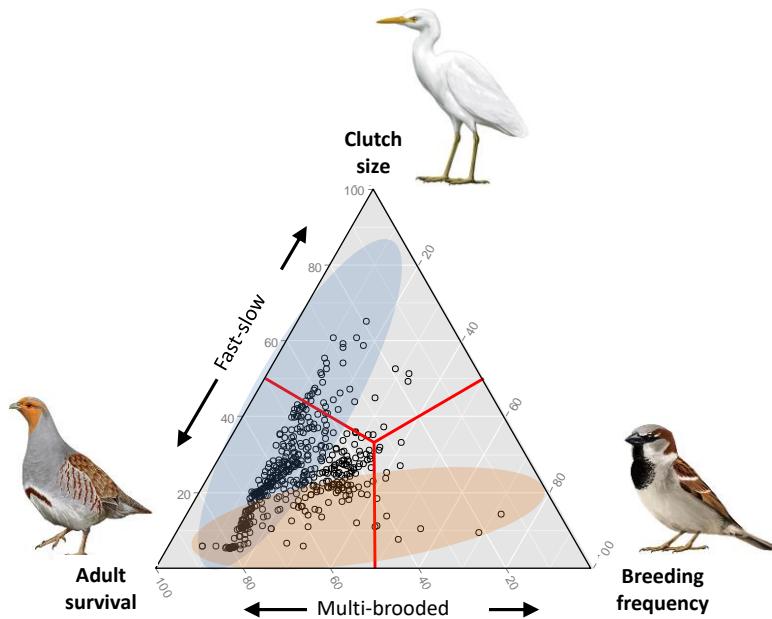


Figure 5.1 Animals exhibit an enormous diversity of life history strategies, which are thought to reflect trade-offs that change the optimal combination of rate of reproduction, age at maturity and longevity with respect to their environments (Stearns, 1992; Roff, 2002). The most well-known trade-off is that between reproduction and survival (Stearns, 1983), which results in a ‘fast–slow’ continuum ranging from organisms with high reproductive rates and low survival prospects (fast lived), at one end, to those that produce few offspring but survive well (slow lived), at the other. While allocating all reproductive effort in a few attempts allows for rapid population growth under favourable conditions, this strategy is risky when conditions are unfavourable because it reduces the chances of breeding again in the future if there is a reproductive failure. A way to maintain a high productivity with a lower cost of losing a breeding attempt is to have multiple broods per year, which defines a second important axis of life history variation.

advantage may be in part countered by a lower risk of extinction through population fluctuations.

Although the population growth and the life history buffer hypotheses are both based on solid demographic theory (Saether *et al.*, 2004), attempts to pinpoint their relative importance on empirical grounds have failed to draw clear conclusions (Blackburn *et al.*, 2009; Sol *et al.*, 2012b). As already advanced, one limitation of these theories is that they assume that demographic stochasticity is the primary source of extinction of introduced populations (Sol *et al.*, 2012b). Demographic stochasticity is certainly important in the invasion process, as suggested by demographic models and by the fact that the likelihood of establishment in introductions increases with the number of individuals released (Cassey *et al.*, 2004; Lockwood *et al.*, 2005). However, if in the new environment individuals cannot find appropriate resources and/or tolerate the physical (e.g. extreme climate) and biotic (e.g. pressure from enemies) adversities, then

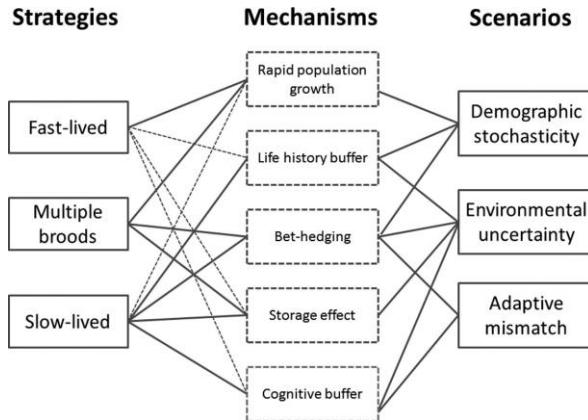


Figure 5.2 Summary of the mechanisms linking life history and invasion success. Continuous lines reflect positive effects and discontinuous lines negative effects. By delineating these mechanisms, we can better infer when it is necessary to consider behaviour.

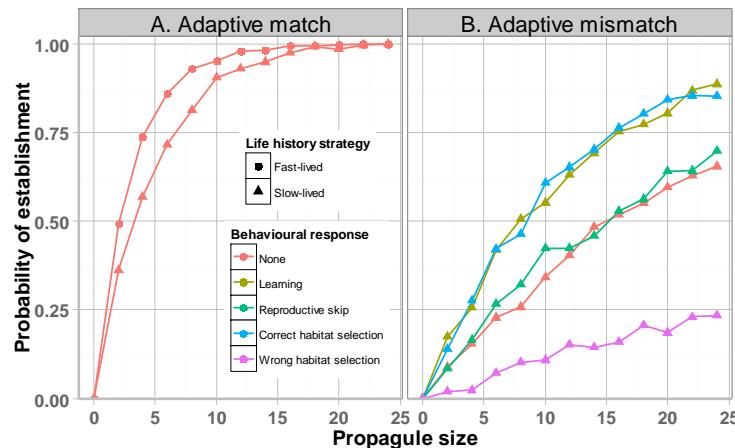


Figure 5.3 Simulations from an agent-based model (Maspons and Sol, unpublished) showing the role of behavioural plasticity in how life history affects establishment success in novel, stochastic environments. The model starts with the introduction of a certain number of adults (propagule size) of a species with a certain life history in a novel environment. The dynamics of each starting population is monitored over time, and the outcome is the proportion of successful simulations per propagule size. In (a), there is no adaptive mismatch and fast-live strategies outperform slow-lived strategies when population size is small. In the (b), the novel region has two habitats, one good and another bad as reflected by differences in adult mortality. This is used to simulate the existence of an adaptive mismatch, which leads to a decrease in population fitness represented by the higher probability of extinction. Through plastic behavioural adjustments individuals may improve their fitness, although only slow-lived animals generally benefit from it. Population fitness improvements may happen if individuals (i) have an innate preference for one of the habitats (activational plasticity); (ii) breed in a different habitat after a reproductive failure (learning); and (iii) can skip a breeding attempt, thereby enhancing survivorship and increasing the time available for exploration. In contrast, an ecological trap can occur if a lack of plasticity in the use of habitat selection cues leads individuals to settle in the wrong habitat.

the more likely is that they have difficulties in surviving and reproducing and that the population goes extinct by negative population growth irrespective of the degree of demographic stochasticity (Figure 5.3). Because invaders come from distant regions and have had little opportunity to adapt to their new environments, the existence of adaptive mismatching should be pervasive in biological invasions. Indeed, some of the best examples of contemporary evolution involve invasive species (Huey *et al.*, 2000; Reznick and Ghalambor, 2001).

The extent to which an invader is in evolutionary disequilibrium depends on whether there is environmental matching between the regions of origin and introduction. If there is environmental matching, then the fitness decrease should be lower as the species would already possess the adaptations needed to persist there (Williamson, 1996). Yet even under such a scenario, a certain decrease in fitness is generally expected as a result of the uncertainties the invader encounters in the novel environment. Uncertainties are generally associated with environmental stochasticity, but can also arise from a lack of information. For an invader, the ignorance about food sources, enemies and other hazards largely increases the risk of reproductive failure and may affect survival as well. This is evidenced by the low success of species that are translocated or reintroduced within their geographic range (Griffin *et al.*, 2000), a result that cannot be attributed to adaptive mismatches. In African elephants (*Loxodonta africana*), for example, individuals that are translocated to new environments for management or conservation purposes exhibit higher death rates than local elephants, in part due to the lack of familiarity of moved individuals with the new habitat (Pinter-Wollman *et al.*, 2009; Figure 5.4). The existence of uncertainties implies that even when an invader is able to proliferate in the new environment, the rate of population growth should be lower than it would be in a more familiar environment. Such a slowdown in population growth should expose the invaders to demographic stochasticity for a longer period, thereby increasing the probability of extinction by accident.

Extending the Classic Framework

By ignoring the importance of environmental uncertainties and adaptive mismatches, the classical framework dismisses the importance of additional mechanisms through which life history can affect invasion success. These mechanisms include bet-hedging, the storage effect and buffer effects associated with certain adaptations (Figure 5.3).

Bet-hedging. This is a strategy to minimize risks that reduces the temporal variance in fitness at the expense of a lowered arithmetic mean fitness (Stearns and Crandall, 1981; Starrfelt and Kokko, 2012). Perhaps the most widespread form of bet-hedging is to distribute the reproductive effort in many events rather than in a few ones, either through a long reproductive life or through a higher frequency of reproductions per year (Figure 5.1). This reduces the variability of the fitness by the law of large numbers, and hence increases geometric population growth. The advantage of multiple reproductions is exemplified in the invasion of an urbanized environment by dark-eyed juncos, which originated from mountainous regions. In their new environment, reproductive success is



Figure 5.4 In slow-lived species, like African elephants, behaviour is expected to play a central role in assisting individuals in novel environments. When translocated to new reserves for management or conservation, the released elephants exhibit higher death rates than local elephants, in part due to the lack of familiarity of individuals with the new habitat. However, behaviour can improve survival at least in two ways. First, individuals tend to settle in habitats that more resembled their natal ones. Second, over time they also tend to converge in behaviour towards that of the local elephants (presumably through social learning). Such behavioural decisions and adjustments allow reducing adaptive mismatch and environmental uncertainties (photograph: D. Sol).

poor yet this can be in part compensated by a higher number of broods per season (Yeh and Price, 2004).

Storage effect. In species that give low value to a breeding attempt, the costs of skipping a reproduction are also reduced. This allows individuals to engage in reproductive activities only when conditions are favourable (Williams, 1966), a phenomenon that in community ecology has been referred to as the storage effect (Warner and Chesson, 1985; Caceres, 1997). Delaying or skipping a breeding attempt has been reported in several long-lived species (Lima, 2009), and can be another life history mechanism to deal with novel situations. As example, Cubaynes *et al.* (2011) reported that red-footed boobies (*Sula sula*) are more likely to skip a breeding event in El-Niño years. This is to be expected if skipping is an adaptive strategy to reduce mortality of adults when the chances of reproducing successfully are low.

Adaptive buffer. Extrinsic mortality differentially affecting juveniles and adults is considered a major driver of life history evolution (Schaffer, 1974; Charlesworth, 1980; Stearns, 1992, 2000; Reznick *et al.*, 2002). A high adult mortality selects for earlier reproduction and higher fecundity so as to reduce the risk of dying without reproducing.

Conversely, a low adult mortality selects for a longer reproductive life. This latter strategy can further evolve when animals develop adaptations that reduce variance in adult mortality (Stearns, 2000). During unfavourable periods, these adaptations can be used to survive until conditions improve. The existence of ‘buffer adaptations’ ensures that survival is high in most years (Morris and Doak, 2004), a requisite for attaining a long reproductive life, and hence may be a mechanism through which life history enhances invasion success. One of the buffer adaptations classically considered in the literature is increased body size, which can provide competitive advantages and protection from enemies. However, evidence that larger species are more successful invaders is contradictory (e.g. Blackburn *et al.*, 2009). Stronger evidence is nonetheless available for behavioural responses, an issue that will be examined in the next sections.

Role of Behaviour in the Response to Novel Environments

Life history theory has largely been developed under the view that organisms are passive subjects of selection. However, behaviour mediates how animals interact with their environment and, by virtue of their plastic nature, can modify the nature of these interactions, shaping the biotic and abiotic pressures that act upon them (Futuyma and Moreno, 1988; Losos *et al.*, 2004). In the next sections, we will discuss the role of behaviour in the response to novel environments, which is essential to better understanding how life history affects invasion success.

In novel environments, animals must decide when and where to breed or what foods are good and what are bad, often with little previous information and lack of specialized adaptations. Behavioural plasticity allows such challenges to be addressed. The idea that behaviour, through cognitive and neural machinery, allows behavioural solutions to unusual or new problems to be devised is known as the cognitive buffer hypothesis (Allman *et al.*, 1993; van Schaik and Deaner, 2003; Sol, 2009a, b).

Mayr (1965) was among the first to propose that plastic behaviours buffer animals when invading novel regions, suggesting that successful invaders should be characterized by a tendency to discover unoccupied habitats and shift habitat preferences. More recent formal developments suggest two forms of behavioural plasticity that are relevant during invasions, namely, activational and developmental plasticity.

Activational Plasticity

Activational plasticity refers to the expression of behaviour and describes the innate response to stimuli that elicit a shift to an alternative behaviour through the activation of a neural network (Snell-Rood, 2013). Because of its immediacy and reversibility, such forms of plasticity allow individuals to efficiently respond to environmental uncertainties by enabling rapid modulation of, or transitions between, behaviours as a function of the individuals’ needs (Snell-Rood, 2013; Sol *et al.*, 2013). These include

fleeing in the presence of a predator, being attracted to new food opportunities and relaxing mate preferences when population density is low.

Activational behavioural plasticity is particularly important in novel environments for its role in mediating habitat and resource choice, which allows environmental uncertainties and adaptive mismatches to be reduced (Figure 5.3). Where the environment is heterogeneous, for example, animals can enhance their fitness by choosing habitats that suit better to their phenotype. Indeed, newly released animals often reject the habitat near the release site and travel long distances away before settling (Stamps and Swaisgood, 2007). They are also often very selective in habitat choice, despite behaving as ecological generalists in their regions of origin. In the highly invasive monk parakeet (*Myiopsitta monachus*), a generalist parrot introduced to Europe and North America, invading individuals not only exhibit a strong tendency to nest in a particular type of tree, even when other suitable trees are also available, but among them they tend to select the tallest ones, perhaps as a way to reduce the risk of unknown predators (Sol *et al.* 1997).

Many animals released in new environments exhibit a consistent preference to settle in familiar types of habitats (i.e. those containing stimuli comparable to those in their natal habitat), a phenomenon called natal habitat preference induction (Stamps and Swaisgood, 2007). In Kenya, for example, elephants that were translocated between reserves tended to settle in habitats that were similar to those used in the source site more than did the local population (Pinter-Wollman *et al.*, 2009). The phenomenon of natal habitat preference induction, as a mechanism promoting niche conservatism, is an effective way to reduce adaptive mismatches and environmental uncertainties.

Animals select their habitats based on a variety of environmental cues that indicate qualities related to their niche requirements. In a novel environment, these cues may change yet they can still be perceived as informative by means of a variety of cognitive processes. Categorization, for example, involves classifying cues based upon perceptual or conceptual similarity (Greggor *et al.*, 2014). This allows discrimination between safe versus unsafe categories so as to minimize costly avoidance behaviours or to selectively respond to particularly dangerous predators (Greggor *et al.*, 2014). However, the risk of perceptual errors can lead to ecological traps (Kokko and Sutherland, 2001; Greggor *et al.*, 2014). Mayflies, for example, use polarized lights to decide where to lay the eggs. Yet, some types of asphalt polarize light horizontally in a way that mimics a highly polarized water surface, and as a result mayflies end up laying their eggs on an inappropriate substrate where they are unable to hatch successfully (Kriska *et al.*, 1998). This later example emphasizes that activational plasticity, being the expression of a prewired genetic programme, is often insufficient to deal with novel challenges (Figure 5.3). However, behaviour can also be plastically modified through developmental mechanisms, which allows further improving the response to novel environmental challenges.

Developmental Behavioural Plasticity

Animals can confront novel challenges, like the need to obtain new types of food or avoid unfamiliar predators, by modifying or inventing behaviours, a process known as developmental behavioural plasticity (Snell-Rood, 2013). Developmental behavioural plasticity is not so immediate as activational plasticity, because it involves changes in the nervous system that alter motor responses. However, it has the advantage that it allows animals to construct responses to unfamiliar or novel problems. One of the main mechanisms behind developmental behavioural plasticity is learning, the acquisition of new information influencing performance in behaviour (Dukas, 1998). Instead of consistently expressing the same behaviour to a particular stimulus, learning allows animals to devise innovative behavioural responses or to improve already established behaviours on the basis of experience (Lefebvre *et al.*, 1997; Dukas, 1998; Reader and Laland, 2002; van Schaik and Deaner, 2003; Ricklefs, 2004). Learning is particularly relevant in facilitating access to novel resources. Over the past years, for example, Lefebvre and co-workers have documented hundreds of observations of animals using novel foraging techniques to exploit foods that would otherwise be difficult to exploit (Lefebvre *et al.*, 1997; Overington *et al.*, 2009). Examples include house sparrows (*Passer domesticus*) using automatic sensors to open a bus station door, green jays (*Cynaoecorax yncas*) using twigs as probes and levers, and herring gulls (*Larus argentatus*) catching small rabbits and killing them in preparation for eating by dropping them on rocks.

Learning can also mitigate the effect of environmental uncertainties in a number of ways. There is, for example, evidence showing that training captive-bred animals to avoid predators or to use food items they are more likely to encounter once released can improve the success of reintroduction programmes (Griffin *et al.*, 2000; Stamps and Swaisgood, 2007). The cognitive processes by which animals can reduce uncertainties include associative and social learning. Associative learning can, for instance, facilitate the use of cues that indirectly predict the presence of predators, including physical cues or the presence of other species (Griffin *et al.*, 2000). Associative learning also allows the incorporation of new cues to assess the quality of unfamiliar habitats. Seppänen *et al.* (2011), for example, showed that European flycatchers (*Ficedula* spp.) can use associative learning to adopt an arbitrary sign situated in a nest-box as a reliable cue of nest site quality. Social learning, on the other hand, can facilitate the transmission of learned behaviours within and among species. The fitness benefits of novel behaviours can for instance be transmitted to other members of the population by this mechanism (Lefebvre, 2013). Social learning can also be important in shaping niche preferences through imprinting or cultural transmission (Slagsvold and Wiebe, 2011). This can favour natal habitat preference induction (Slagsvold and Wiebe, 2007). By means of a cross-fostering experiment between blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*), Slagsvold and Wiebe (2007) demonstrated that early learning can cause a shift in the feeding niche in the direction of the foster species. Some animals may even adopt new cues to assess habitat quality based on public information inadvertently produced by the presence or breeding performance of individuals of other species with similar environmental needs (Danchin *et al.*, 2004; Parejo *et al.*, 2008).

Evidence for a Role of Behavioural Plasticity in the Invasion Process

Although the hypothesis that plastic behaviours can assist animals in invading novel regions dates back from Mayr (1965), until recently the hypothesis was backed by little empirical evidence. Recent attempts to explore the issue have progressed in three distinct directions. The first is based on broad comparative analyses of historical introductions of animals outside their native ranges. While such historical data have certain limitations, reliable results may still be obtained by using appropriate modelling techniques that control for the effects of introduction effort and other confounding factors (Sol *et al.*, 2007b). The analysis of such quasi-experimental data has revealed that the propensity to invent new behaviours and/or the underlying neural substrate (see next section) enhance the likelihood of establishment in novel environments in birds, mammals, reptiles and amphibians (Sol *et al.*, 2005, 2008; Amiel *et al.*, 2011). Evidence is, however, absent for fish (Drake, 2007).

The second approach to exploring the role of behavioural plasticity in invasion success has focused on evaluating whether behavioural adjustments are necessary in the situations where invaders attain higher success. For example, many vertebrate invaders attain higher densities in human-altered habitats than in more natural habitats, and there is ample evidence that living in these environments often requires changes in behaviour (Lowry *et al.*, 2012; Sol *et al.*, 2013). Thus, urban animals frequently differ in foraging behaviour (e.g. more readily adopting new foods derived from human activities or developing new foraging techniques), activity patterns (e.g. reducing flight initiation distances or becoming more active during the night) and even in the way they communicate with others (e.g. reducing song frequency in noisy places or singing in the dawn) relative to those from surrounding habitats. Although some of these behavioural differences can reflect evolutionary responses or a sorting process (in which only individuals with proper behaviours are able to colonize the environment), others can unambiguously be attributed to behavioural plasticity (Sol *et al.*, 2013). Laboratory experiments on common mynas (*Sturnus tristis*) introduced to Australia have, for instance, revealed that the species has a remarkable ability to explore and adopt new food types, and that these cognitive abilities are more pronounced in individuals inhabiting the disturbed habitats in which they attain higher success (Sol *et al.*, 2011, 2012a).

The last approach providing insight into the role of behavioural plasticity in the invasion process consists of examining differences in key components of behavioural plasticity between populations of a same species exposed to conditions in which plasticity is expected to be either highly or little relevant. A classic example is the reduction in intraspecific aggression observed in some invasive ants, which has contributed to their invasion success by favouring expansive supercolonies (Holway and Suarez, 1999). Other examples include experiments in birds measuring plasticity in invasive and noninvasive populations. For example, experiments in house sparrows introduced to North America suggest that individuals that are invading a new region are more likely to approach and consume novel foods than those that have been in the region for a longer time (Martin and Fitzgerald, 2005). This latter result can be interpreted in

terms of the costs of behavioural plasticity, which predicts that selection should reduce plasticity over time as the invader increasingly becomes locally adapted.

Why do we Need Behaviour to Better Understand how Life History Affects Invasion Success?

Behaviour cannot be ignored as one of the mechanisms by which life history affects invasion success for two main reasons. First, behavioural plasticity is not only an important mechanism of response to novel challenges but its benefits depend on the species' life history. Second, behaviour directly mediates some life history mechanisms, particularly those related to environmental uncertainty and adaptive mismatch like the storage effect and bet-hedging. We will examine both issues in the next sections.

Behavioural Plasticity and the Fast–Slow Continuum

The fast–slow continuum implies a differential need to collect and use information (van Schaik and Deaner, 2003; Sol, 2009a; Sih and Del Giudice, 2012). Animals at the ‘slow’ extreme of the fast–slow continuum tend to explore more accurately and often exhibit better performance in problem solving and learning. One reason is that they tend to have disproportionately larger brains, which has been shown to enhance the capacity to innovate and learn (Lefebvre *et al.*, 1997; Reader and Laland, 2002; Overington *et al.*, 2009; Reader *et al.*, 2011) as well as improving survival prospects (Sol *et al.*, 2007a; Kotrschal *et al.*, 2015). Although a slow life history can be developed with no need of a large brain, a large brain can only evolve in animals at the slow extreme of the fast–slow continuum. This is because a large brain takes longer to grow, and hence imposes a developmental constraint in terms of extended growth and maturation (Barton and Capellini, 2011). In addition, the benefits of large brains in providing a ‘cognitive buffer’ against sources of extrinsic mortality should select for and be selected by a slower life history (Allman, 2000; van Schaik and Deaner, 2003; Sol, 2009a, b). Exploring and learning about the environment is more beneficial for a long-lived than for short-lived species because individuals are more likely to be exposed to environmental changes during their lifetime. In addition, the learned behaviours can provide benefits for longer periods. The costs are also reduced, at least in terms of time constraints. Having more time allows animals gathering more and better information, improving decision-making (Stamps *et al.*, 2005, Mabry and Stamps, 2008) and problem solving.

Nevertheless, animals with high future reproductive prospects are more likely to develop risk-averse behaviours. In a novel environment, this should affect how they resolve the conflict between the need to approach and to explore new resource opportunities and, at the same time, avoid unnecessary risks (Greenberg, 2003; Sol *et al.*, 2011). While this could compromise their chances of succeeding in the new environment, this is not necessarily true for two reasons. First, the balance between approach and avoidance is expected to differ depending on the environmental context.

For example, in urbanized environments where exposure to novel feeding opportunities is commonplace and risks associated with specialized predators are low, invaders should generally favour exploration over avoidance (Sol *et al.*, 2011). Common mynas introduced to Australia fit well with this expectation, exhibiting lower neophobia and higher neophilia in highly urbanized environments (Sol *et al.*, 2011). Second, both theoretical and empirical evidence suggest that risk-averse animals should explore slowly but more accurately (Marchetti and Drent, 2000). This is because the existence of a speed–accuracy trade-off that improves accuracy when exploration is slower (Sih and Del Giudice, 2012). Thus, a risk-averse strategy does not necessarily prevent the animal from adopting novel ecological opportunities and successfully establishing in the new environment.

Behavioural Plasticity and Life History Mechanisms

Plastic behavioural responses can mediate life history mechanisms affecting success in novel or uncertain environments in a variety of ways. This is clear for the storage effect, as the decision whether to breed or not when conditions are uncertain is itself a behavioural decision. Skipping a reproduction also provides more time for exploring the new environment and adjusting behaviour through learning (Figure 5.3).

Understanding bet-hedging mechanisms can also benefit from considering behavioural responses. Learning, in particular, can improve breeding performance in species that spread the risk of reproductive failure over several breeding attempts. A change in nest site choice is a well-documented response to nest predation (Lima, 2009). In the Brewer's sparrow (*Spizella breweri*), for example, the cost of a reproductive failure is compensated in part by new nesting attempts (Chalfoun and Martin, 2010). However, previous experience largely modifies subsequent breeding decisions. Thus, pairs move sequential nest sites slightly farther away from their initial site following an episode of nest predation. Moreover, they also change nest patch attributes (e.g. shrub height, shrub density) to a greater extent following nest predation.

Finally, behaviour may affect predictions derived from the small population paradigm. In experimental field introductions of the Argentine ant (*Linepithema humile*), Sagata and Lester (2009) found that propagule pressure was a relatively poor predictor of establishment success owing to the ability of this species to modify its behaviour according to environmental conditions and resource availability. By shaping the extent to which the population is affected by Allee effects, some behaviours can also influence the susceptibility of the population to extinction by demographic stochasticity. Blackburn *et al.* (2009) found that species that can reduce Allee effects through behaviours like dispersal tendency or mate choice are more likely to establish successfully in new environments.

Concluding Remarks

To characterize the life history of successful invaders, classical theory emphasizes the importance of life history mechanisms related to small population dynamics. While we do not deny the importance of these mechanisms, we highlight here the need to also consider alternative mechanisms related to responses to adaptive mismatches and environmental uncertainties. This forces us to take into consideration the role of behaviour.

By its plastic nature, behaviour acts to reduce environmental uncertainties and adaptive mismatches, thereby directly affecting invasion success. However, the importance of behaviour is not the same for all life history strategies. Those that give more value to adults than to offspring presumably benefit more from behavioural plasticity because are more likely to possess the adaptive machinery underlying plastic responses and have more opportunities to assemble and respond to environmental information. The connection between behaviour and life history suggests thus that both should be considered as part of a same adaptive strategy of response to environmental changes. This idea is further emphasized when considering that behaviour can also mediate some of the mechanisms by which life history influences the response to novel environments, notably the storage effect and bet-hedging.

The existence of a variety of mechanisms by which life history and behavioural plasticity affects population dynamics in novel environments suggests that there is no single strategy to be a successful invader. Thus, the optimal strategy can vary according to the degree of demographic stochasticity, adaptive mismatch and environmental uncertainty (Figure 5.2). This may explain why unravelling the life history of successful invaders has proved difficult. Despite this, if some scenarios are more frequent than others we can still make some generalizations regarding the life history strategies of successful invaders. In vertebrates, for example, many invaders are primarily restricted to human-altered environments (Case, 1996; Sol *et al.*, 2012a; Barnagaud *et al.*, 2013), which facilitate invasions by simultaneously opening new resource opportunities and decreasing the pressure of competition and predation from native species. In these environments, animals are continuously exposed to novel ecological challenges and uncertainties, which should favour a ‘slower’ strategy of high future reproductive prospects. Indeed, a recent global comparative analysis of avian introductions evidenced that although rapid population growth may be advantageous during invasions when propagule pressure is low, successful invaders are generally characterized by life history strategies in which individuals give priority to future rather than current reproduction, either by means a long reproductive life or a higher frequency of reproductions (Sol *et al.*, 2012b). The more recent finding that urban dwellers also tend to spread reproductive effort across many breeding attempts (Sol *et al.*, 2014) further confirms the importance of this strategy in dealing with environmental uncertainties and adaptive mismatches.

Despite progress, there remain important issues to resolve to better integrate behaviour into a life history framework for biological invasions. A first issue that requires further attention is how cognition is functionally related to variation in life

history, and how together these mediate the response of organisms to environmental changes. In this chapter, we have described several such mechanisms, yet others are also possible. For example, animals with enhanced learning abilities tend to be highly social, whether because sociality selects for these abilities (Shultz and Dunbar, 2007) or because both characteristics are a by-product of selection for longer lives (Sol, 2009b). The social environment might further buffer inexperienced individuals in adverse conditions by facilitating behavioural innovations (Liker and Bókony, 2009; Morand-Ferron and Quinn, 2011) and reducing predation risk (Krams *et al.*, 2010). To date, however, the importance of sociality during the invasion process has been difficult to evaluate because most introduced animals tend to be social.

The second important issue to resolve is the extent to which life history trade-offs are stable or can be relaxed or even broken. Although the existence of trade-offs is undisputed (Stearns, 1992; Roff, 2002), there are a number of situations that can relax the trade-offs and even change their sign (Stearns, 1989), notably the existence of genotype \times environment interactions (Reznick *et al.*, 2000). In addition, natural populations often consist of phenotypically diverse individuals (Araújo *et al.*, 2011), a situation we have largely ignored in this chapter. The existence of individual differences in life history and behaviour (e.g. Réale *et al.*, 2007; Biro and Stamps, 2008; Bolnick *et al.*, 2011; González-Suárez and Revilla, 2013a) can generate variation in the demographic parameters of the population, potentially affecting success in novel environments (Bolnick *et al.*, 2011; Phillips and Suarez, 2012). Interestingly, theoretical developments predict that variation in life history and behavioural types should be linked. Biro and Stamps (2008), for example, suggested that variation in exploratory behaviour can be maintained by trade-offs between early and late fecundity. Likewise, Wolf *et al.* (2007) argued that animals varying in future prospects are more likely to develop differences in risk-averse behaviours, which can lead to stable individual variation in aggressiveness and boldness. All these complexities need to be accommodated in a more general theory.

The last aspect for resolution is the extent to which the life history of the invader can evolve towards the optimal strategy for the novel environment. Life history is known to evolve quickly in some invaders following trajectories predicted by life history theory (Huey *et al.*, 2000; Reznick and Ghalambor, 2001; Reznick *et al.*, 2008), yet whether these changes are sufficient to deal with the pressures of novel environments is less clear. Moreover, if individuals respond behaviourally to the new challenges this can hide genetic variation from selection and slow down the adaptation process (Huey *et al.*, 2003). Yet, if responding behaviourally to the most common challenges hides genetic variation from selection, this should enhance the genetic variation available for selection when conditions are more adverse and behavioural responses are less efficient.

These and other potentially fruitful areas of research, if pursued, have the power to reshape the field in the near future, shedding new light into the importance of behaviour in biological invasions and, more generally, contributing to better understand the response of animals to human-induced rapid environmental changes.

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