Can behavioral and personality traits influence the success of unintentional species introductions?

David G. Chapple, Sarah M. Simmonds and Bob B.M. Wong

School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia

Unintentional species invasions are instigated by human-mediated dispersal of individuals beyond their native range. Although most introductions fail at the first hurdle, a select subset pass through each stage of the introduction process (i.e. transport, introduction, establishment and spread) to become successful invaders. Efforts to identify the traits associated with invasion success have predominately focused on deliberate introductions, which essentially bypass the initial introduction stage. Here, we highlight how behavior influences the success or failure of unintentional species introductions across each stage of the introduction process, with a particular focus on transportation and initial establishment. In addition, we emphasize how recent advances in understanding of animal personalities and individual-level behavioral variation can help elucidate the mechanisms underlying the success of stowaways.

Behavior: an important factor in the success of invasive species?

Each day, human activities lead to the inadvertent movement of individuals from thousands of different species to regions outside their native range [1–4]. These stowaways are not a random representation of the biodiversity of the world [5,6], as the 'opportunity' of a species for transportation is influenced by its proximity to human-occupied environments or transport hubs (see Glossary), and the frequency and nature of the trade routes between regions [7–9]. Only a small subset of individuals that are unintentionally transported to new regions manage to pass successfully through each stage of the introduction process to become invasive ([10], Figure 1, Table 1). Given such variability in the success of introductions, a central focus of invasion biology is to identify the traits or factors that accurately predict the ultimate fate of stowaways [11,12].

Researchers recognize several species-level traits (e.g. life-history, habitat generalist and diet) that appear to predict introduction success reliably within particular taxonomic groups, but have been frustrated by the lack of consistency in the specific traits identified among groups [5,11,12]. However, propagule pressure has emerged as a more general determinant of establishment and invasion success in most animal groups [13,14]. Although the propagule pressure concept is enticing and deceptively simple (i.e. introducing more individuals to an area increases the likelihood of successful establishment [13–15]), the behavioral mechanisms that lead to the unintentional movement of individuals are more complex and have rarely been considered. Behavior mediates how animals interact with their environment and should therefore have a pivotal role in the tendency for individuals to be transported and their ability to transition through the various stages of the introduction process.

Indeed, the inclusion of behavioral traits improves predictions of establishment success [7,16–18], but specific information on behavior is often lacking for many species [19]. A decade ago, a review by Holway and Suarez [20] focused on the role of behavior in the post-establishment phase of the introduction process. Their review was the catalyst for numerous studies that have advanced understanding of how newly established species (through a combination of pre-existing traits, behavioral plasticity and trait evolution) can successfully outcompete native species and expand their range. Nevertheless, the role of behavior during the crucial transportation and initial establishment stages has been largely neglected. Given that the relative importance of unintentional introductions is steadily increasing owing to globalization and the associated movement of people and cargo [3,8,21], a better understanding is needed of the factors influencing the propensity for species to be transported via human-mediated dispersal. Although invasion success is ultimately dependent on a range of traits and factors (e.g. life-history,

Glossary

Allee effect: a biological effect, named after Warder Allee, where aspects of fitness are reduced when the population size is low.
Behavioral syndrome: a suite of correlated behaviors that is exhibited across different situations or contexts.
Introduction process: a series of sequential stages (transport, introduction, establishment and spread) through which individuals or populations need to pass to be considered invasive.
Invasion syndrome: a series of correlated traits, particularly behaviors, that enhance transition success across multiple stages of the introduction process.
Propagule pressure: a composite measure of the number of individuals in each introduction event (propagule size) and the number of separate introductions (propagule number) for a given species in a particular recipient region.
Transport hub: a region or locality that constitutes the point of origin, transit link, or destination for one or more modes of transport (e.g. road, rail, air or sea).
Transport vector: the vehicle or transport method (e.g. cargo ship, truck, airplane or train) that moves individuals between two regions. This may involve transport from the native range to a new region, or between two non-native regions.

Corresponding author: Chapple, D.G. (David.Chapple@monash.edu)

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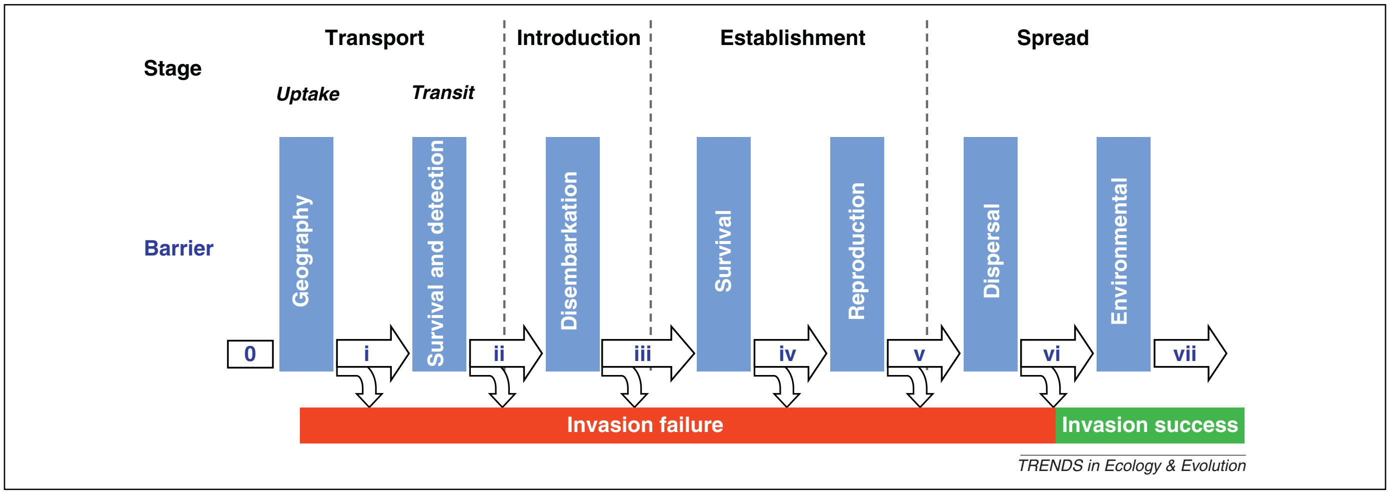

Figure 1. An outline of the invasion process for unintentional species introductions. Our scheme follows the proposed unified framework for biological invasions developed by Blackburn *et al.* [10], but with a specific focus on accidental introductions. The invasion process involves a series of sequential stages (transport, introduction, establishment and spread) through which the stowaways need to transition to become successful invaders. Each stage contains one or more barriers that must be overcome to transition through to the next stage. Invasive species are those that have successfully negotiated their way through each stage and/or barrier and spread throughout the recipient region. The arrows indicate the progression of individuals through the introduction process, with the roman numerals detailing the specific steps on the pathway to invasion success outlined in Table 1 (main text). Adapted, with permission, from [10].

propagule pressure and climatic match), here we: outline a framework for investigating how behavior influences the success or failure of unintentional species introductions; highlight the importance of the early stages of the introduction process in invasion success; and emphasize how advances in understanding of animal personalities and individual-level behavioral variation can help elucidate the mechanisms underlying the success of stowaways.

The key to invasion success appears to lie in the initial stages of the introduction process

There are two inconvenient truths in invasion biology. First, most research has concentrated on the latter stages of the introduction process [5,22,23]. Second, most investigations of invasion success have focused on deliberate introductions, or a combination of deliberate and accidental introductions [11,12]. The transport and introduction phases of the introduction process are important, as transition success is lowest during this period (i.e. it is where most unintentional introductions fail) [11,22,24]. Deliberate introductions bypass this stage and represent a biased subset of species (i.e. those selected by humans owing to specific traits) that have not been through the transport 'filter' [7,25,26]. Analysis of deliberate introductions may therefore provide only limited insight into how species are inadvertently transported and what influences their chances of establishment [23]. This is not a trivial concern, as relatively few studies investigating the determinants of establishment success (including those highlighting the importance of propagule pressure) have focused solely on unintentional introductions [12]. For these reasons, relatively few studies have investigated the behavioral traits that assist the successful passage of individuals through the initial stages of the introduction process. We argue that such studies are important and provide a framework for research into the behavioral traits that may act to enhance success at each stage of the introduction process.

Table 1. Steps in the pathway to the success of unintentional species invasions[a]

Step	Explanation
0	Individuals in their native range that have not entered a transport vector
i	Individuals that have entered a transport vector and are en route to a destination beyond the limits of their native range
ii	Individuals within a transport vector that have survived transit and reached the non-native destination without detection[b]
iii	Individuals that have disembarked from the transport vector and continue to evade detection
iv	Individuals that are capable of surviving and go on to reproduce[b]
v	Individuals that are capable of surviving, reproducing and maintaining a self-sustaining population in the non-native region[b]
vi	A self-sustaining introduced population where individuals are able to survive and reproduce beyond the origin area of introduction[b]
vii	An invasive species where individuals are capable of dispersing, surviving and reproducing at multiple localities across the introduced region

[a]Modified, with permission, from [10].

[b]Failure to survive or reproduce may be because of natural processes or management efforts.

What behaviors might enhance success at each stage of the introduction process?

At present, there is no comprehensive list of potential behaviors that might be associated with invasion success [27]. Previous studies have sometimes been able to identify key behavioral traits among a broader list of characteristics or factors that may improve invasion success [5,7,11,12,16–18]. However, most studies have focused either on specific taxonomic groups [28,29], or only mentioned behavior anecdotally [30,31]. Aside from some notable exceptions [5], behavioral traits have only been related to one specific stage (if at all). Based on the published literature, we compiled a detailed list of behaviors that may contribute to unintentional introductions

Table 2. Potential behaviors that can influence success of unintentional species introductions at each stage of the introduction process[a]

Behavioral trait[b]	Transport		Introduction	Establishment	Spread	Refs
	Uptake	Transit				
Actively hide and/or seek shelter	+[c]	+[c]	+/–	–	+[c]	[30,32,78]
Activity	+	–	+	+	+[c]	[33]
Antipredator behavior[1]	?	?	?	+/–	+/–	[29,31,58,65,90]
Antiparasite behavior	?	?	?	+/–	+/–	[72]
Attraction to and/or tolerance of human-occupied environments	+	?	+	+[c]	+/–	[16,20,37,40]
Boldness[1,4,5]	+	–	+	+	+[c]	[33,40,65,88]
Dispersal tendency[3,4,5]	+	–	+	+/–[c]	+[c]	[18,29,33,57,61,63,80,82–84,88]
Exploratory behavior[4]	+[c]	–	+	+/–[c]	+[c]	[31–33,71,91]
Foraging behavior and flexibility[1,2]	+	?	+	+[c]	+	[18,29,31,58,59,65,66,71]
Habitat preferences and flexibility	+	+	+	+[c]	+[c]	[18,29,31,36,37]
Intraspecific aggression[1,2,4]	–	–	–	–[c]	+/–[c]	[20,29,31,46,48–50,52,55,65,66,70]
Interspecific aggression[3]	?	?	+	+[c]	+[c]	[20,29,51,53,54,60,61,64,70,83,84]
Mate choice and recognition	?	?	?	+/–[c]	+/–[c]	[18,92]
Nesting and/or oviposition behavior	+[c]	?	?	+[c]	+[c]	[7,16,37,46,50,51]
Parental care	+	+	?	+	+	
Social tendency[4,5]	+	+/–	+	+[c]	+/–[c]	[33,48,88]
Species recognition	?	?	+	+	+	
Thermoregulatory behavior and flexibility	+	+	+	+	+	[36,93,94]

[a]These behaviors may have either a positive or negative impact on success. The Refs column indicates the studies that have examined the role of the behavior during the introduction process. Only studies since the review by Holway and Suarez [20] have been included.

[b]The numbers indicate which behaviors have been linked in a behavioral syndrome in invasive species: 1, [65]; 2, [66]; 3, [84]; 4, [33]; 5, [88].

[c]At least one empirical study has indicated that this behavior is associated with success at this stage in the introduction process.

successfully transitioning through each phase of the introduction process (Table 2). Success at particular stages may be related to the presence of pre-existing behavioral traits or be the result of the capacity for phenotypic plasticity or adaptability in these traits [6].

As the factors that convey success at each introduction stage differ [5,6,11], certain behaviors may have a complementary influence across multiple stages, but counteractive impacts may also occur between stages. For instance, exploratory behaviour may not only enhance the likelihood of uptake into transport vectors and the subsequent establishment and spread in the recipient region, but might also increase the risk of detection by biosecurity checks during transit (e.g. *Lampropholis* lizards [32]). Similarly, species that exhibit strong dispersal tendencies could also be less social (e.g. mosquitofish, *Gambusia affinis* [33]), which might then enhance their susceptibility to Allee effects during the establishment and spread stages [34,35].

Here, we outline how behavior can influence the success of unintentional introductions, using the recently developed framework for biological invasions ([10], Figure 1). Although we focus on unintentional introductions, owing to the limited number of studies in this area we also draw upon the broader invasive species literature, including, where appropriate, studies that have been carried out on species that have been deliberately introduced.

Stage 1: uptake and transportation

All unintentional species introductions have a beginning, and rely upon individuals becoming ensnared within a transport vector. Human-assisted dispersal enables stowaways to overcome geographic barriers and move to new areas beyond their native range ([10], Figure 1). Most species have never been accidentally transported to non-native regions, as not all species have the equivalent 'opportunity' for uptake into transport vectors [7,26]. It has been hypothesized that invasive species are more likely to have experienced an evolutionary history of environmental disturbance in their native range, and are likely to be generalists with broad (or flexible) habitat, dietary and thermal preferences or tolerances [6,36,37]. Such species are likely to occur in high densities in human-occupied environments and have widespread distributions that overlap with multiple transport hubs, enhancing their opportunity for transportation [8,23,26,30,32].

For those species that have the opportunity for transportation, the 'uptake' of individuals into transport vectors may occur through either passive or active means. Passive uptake may occur where animals reside or shelter within valuable commodities (e.g. fresh produce, timber, soil and plant and/or garden materials) that are transported between regions [8,30], or enter ships in ballast water [23]. Many of the most common stowaways (e.g. frogs in bananas, ants in soil or invertebrates in timber shipments) may become ensnared within transport vectors as an indirect result of their preference or association with a particular commodity [21,24,30,38].

Behaviors that can enhance the likelihood of passive uptake include actively hiding or sheltering, habitat preferences, foraging behavior, nesting behavior, sociality and thermoregulation (Table 2). Although investigations of the determinants of introduction success have highlighted the importance of several of these behaviors [7,18], we are only aware of one study [32] that has adopted a comparative experimental approach (e.g. [39]) to demonstrate whether the propensity for transportation is related to variation in these behaviors between invasive and non-invasive species.

Opportunities for stowaways to enter freight and cargo actively also exist during transit or storage in warehouses, wharfs, transport yards and loading docks [8,30]. The likelihood of individuals entering freight and cargo is highly dependent on both the location and duration of its storage [8,30]. Animals living in urban environments are often more bold and exploratory [40,41], and these behaviors may result in individuals actively searching and finding their way into freight, cargo or personal effects [9,42]. Activity, boldness, dispersal tendency and exploratory behavior are all traits that have been linked to invasiveness at later stages of the introduction process (Table 2), but we know of only one study [32] that has specifically investigated whether such behaviors increase the incidence with which species are inadvertently transported to new locations. In this regard, a range of other behaviors may also be important (Table 2).

Species that have a high propensity for uptake into transport vectors will be frequently transported to new regions. A tendency for human-assisted dispersal of individuals, particularly in large groups, may act to increase the propagule pressure for the species [13–15]. However, this will only be true if individuals are able to avoid detection, survive transit and arrive in good health [3,10,14]. The conditions to which the stowaways are exposed (e.g. space, temperature, oxygen level, and availability of food and water) during transit will be strongly influenced by the type of transport vector involved [8,43,44]. Similarly, transit time is dependent on the distance between the origin and destination, and the mode of transportation [8,30,44]. Although increase in air transport over the past century has dramatically decreased the transit time between regions, its cargo capacity is substantially less than for sea transport [8,44]. Thus, behaviors that contribute to survival during transit may be context dependent; however, species that exhibit a tendency to seek shelter, are able to regulate their body temperature in suboptimal conditions (e.g. by forming aggregations), or can locate food items in novel environments are expected to be favored ([5], Table 2).

The detection of stowaways in freight, cargo or personal effects is likely to lead to the individuals being retained in captivity or destroyed (e.g. fumigation) [2]. However, evidence suggests that even the most rigorous biosecurity protocols and checks may detect less than half of all the hitchhikers within a consignment [24,30]. Thus, species that actively hide or shelter, particularly within structurally complex freight or cargo, are more likely to evade detection during transit [24,30,32,45]. A variety of invertebrate (e.g. insects and spiders) and vertebrate groups (e.g. squamate reptiles and amphibians) are proficient in avoiding detection during transit through such behaviors [21,30,32,45,46]. For example, it is believed that brown tree snakes (*Boiga irregularis*) were accidentally introduced to Guam as a result of individuals sheltering within military equipment transported to the island shortly after World War II [21,47]. Interestingly, several of the behaviors that may facilitate the initial uptake of individuals into a transport vector (e.g. activity, boldness, dispersal tendency, exploratory behavior and social tendency) may increase the risk of detection during transit (Table 2). Experimental investigation of how particular behaviors increase survival and the ability to evade detection represents a productive area for future research [32], and may also aid in the development of strategies to improve biosecurity protocols and techniques to treat contaminated cargo.

Stage 2: introduction

The introduction process framework developed by Blackburn and colleagues [10] was designed to encompass deliberate introductions where release into the recipient region may require escape from captivity or cultivation. However, for unintentional introductions, this stage simply involves the individuals disembarking from the freight and/or cargo or transport vector (Figure 1). Intuitively, disembarkation should be the reverse of uptake, with individuals using the same suite of behaviors (e.g. exploratory behavior) to exit the transport vector and enter the new environment (Table 2). Although stowaways may be deposited in the first port within the new region, freight and/or cargo or personal effects are often transported within the recipient region via road, rail, air or rivers and/or canals [8,44]. Upon arrival at the destination, the individuals need to disembark, explore the new environment and seek out food, warmth and suitable habitats [5] (Table 2). The stowaways will generally be deposited into urban areas, with environments to which they may be well adapted [6,36]. Importantly, individuals will need to continue to avoid detection post-border to ensure success at this stage.

Stage 3: establishment

Successful establishment in a non-native area requires the incipient population to survive and reproduce [10] (Figure 1). Positive population growth is essential not only for establishment, but also for subsequent spread across the landscape. To date, most behavioral research on invasive species has focused on the post-establishment and spread stages of the introduction process (Table 2). Concentrating mostly on invasive ants [46,48–55], lizards [40,56], fish [57–59] and crustaceans [29,60–66], these studies have shown that successful invaders often exhibit high levels of interspecific aggression and are able to outcompete native species for space and resources [20]. However, the behavioral processes that enable the initial establishment of populations in new regions have largely been neglected.

The transportation process generally results in the introduction of single individuals or small groups [24,45,67], which arrive at different times and often from multiple regions of the native range [14,68]. There is an implicit assumption, which has rarely been investigated, that individuals from temporally or spatially separated propagules will be capable of locating, recognizing and interacting with each other in the introduced region [5,13,14]. In the incipient population, the presence of propagules originating from different regions of the native range will require individuals to use a range of behaviors to facilitate appropriate interactions (e.g. social group formation, antipredator behavior, intraspecific aggression and species recognition) and reproductive activities (e.g. mate choice, nesting behaviour and parental care) with conspecifics that may have been reproductively isolated for millions of years. Failure to do so could lead to a small population size and leave the incipient population susceptible to demographic or environmental stochasticity and Allee effects [34,35].

In a study of deliberate bird introductions, species that can reduce Allee effects through their behavior (e.g. dispersal tendency or mate choice) are more likely to establish successfully in new environments [18]. Although theoretical models suggest that high propagule pressure can counteract the impacts of Allee effects and enhance establishment success (e.g. spruce bark beetles, *Ips amitinus* [69]), population size is not the sole determinant of success. For example, propagule pressure has been shown to be a relatively poor predictor of establishment success in experimental field introductions of the Argentine ant (*Linepithema humile*), owing to the ability of this species to modify its behavior according to environment conditions and resource availability [70]. As a result, propagule pressure may not be a strong determinant of establishment in species that exhibit behavioral plasticity [70].

Nevertheless, behavioral flexibility has been identified as one of the key traits contributing to the success of invasive species [31]. During the introduction process, stowaways are exposed to a variety of novel environments, food items, predators, and parasites or pathogens [71,72]. Species with larger brains are predicted to exhibit increased behavioral plasticity and an enhanced capacity to negotiate the challenges inherent during the introduction process [73]. Indeed, comparative analyses using species introduction databases have found that successful invaders have larger relative brain size compared with those that fail to establish in new regions; a pattern that has been reported in birds [16], mammals [17], amphibians and reptiles [74]. It remains unclear whether the degree of brain specialization or size *per se* promotes behavioral flexibility [74], but it is a question that deserves further research attention.

Stage 4: spread

Many populations that successfully establish in a new region experience a lag phase before spreading out across the non-native region [2,27,75]. The delay in population spread may be the result of the time required for sufficient population growth, adaptation to the new environment, augmentation of genetic variation, or a shift in the interactions with native biota [2,27,76]. A substantial amount of behavioral research has focused on species interactions (e.g. aggression or competition) as the invader moves through the landscape [20] (Table 2). Here, we focus on the dispersal mechanisms responsible for population spread (Figure 1).

Rapid geographic spread generally requires the species to overcome environmental barriers and move from human-occupied regions into rural or natural habitats [10]. Population spread can be achieved through either natural or human-assisted dispersal [8,9,27,77]. Intuitively, behavioral traits (e.g. exploratory behavior, actively hide and/or shelter, and habitat preferences) that facilitated the initial uptake and transportation of stowaways should act to promote human-mediated movement of individuals within the introduced region. This may enable invasive species to spread rapidly between human-inhabited regions and result in repeated 'spot-fire' introductions of the species across its invasive range. For example, fire ants (*Solenopsis invicta*) were transported to new areas in Florida during road maintenance activities owing to the use of soil from a contaminated central depot [38]. Such a dispersal mechanism also enables species that have limited natural dispersal abilities, such as land snails (*Xeropicta derbentina*), to spread quickly through the introduced region [78]. However, even invasive species that are renowned for their natural dispersal abilities (e.g. the cane toad, *Bufo marinus*) have been demonstrated to be adept at human-assisted dispersal [79].

Recently, theoretical and empirical studies have enhanced understanding of the mechanisms that drive the 'natural' dispersal of invasive species throughout their introduced range [6,27,80–82]. Field and laboratory-based investigations of invasive species have found links between dispersal and behavioral traits, such as boldness, aggression and exploratory behavior. Invasive mosquitofish species exhibit a greater tendency for dispersal compared with their non-invasive congeners [57]. Similarly, aggression and dispersal tendency was closely coupled in western bluebirds (*Sialia mexicana*), facilitating both range expansion of the species and displacement of a less aggressive congener [83,84].

Behavior, personality and the existence of invasion syndromes

It is a key, but seldom emphasized, fact that not all individuals of a population or species get transported or transition through a particular stage of the introduction process. As our review has highlighted, only a subset of individuals manage to negotiate any given stage successfully, and invasion success involves passing through a series of sequential stages (Figure 1). Hence, the introduction process acts as a 'selective filter' [26,27]. Although most attempts to identify the determinants of invasion success have focused on species-level traits, recent research has indicated that intraspecific variation in behavioral traits may act to enhance the invasion potential of a species [42,85,86].

Over the past decade, there has been considerable interest in animal personalities or behavioral syndromes, the idea that suites of behaviors are often correlated [42,85,87]. Such syndromes can involve either positive or negative correlations among traits, with individuals exhibiting a consistent behavioral type (e.g. active, aggressive and bold) across several different situations or contexts [42,85]. As we have emphasized, invasion success requires individuals to transition through each and every stage, and stumbling at any stage will result in failure [10]. Although each stage of the introduction process has its own distinct set of obstacles and challenges (Figure 1), some behavioral traits may be advantageous across multiple stages. For example, individuals that are aggressive are generally more bold and exploratory [33,57] and this may assist in getting transported, dispersing and outcompeting native

Box 1. Behavioral syndromes: a key to understanding invasion success?

Individual variation in personality traits (behavioral syndromes) can influence the success of introduced species. However, to date, only a handful of studies have explicitly investigated behavioral syndromes in the context of species invasions, and all have focused on deliberately introduced species during the establishment or spread stage.

Successful invasive species are often highly aggressive, a behavioral trait that is expected to result in strong intraspecific competition. Despite this, successful invaders often occur at extremely high densities. Pintor and colleagues [66] found evidence for an aggression syndrome in the invasive signal crayfish (*Pacifastasus leniusculus*) that may help explain its superabundance in invasive regions. Mesocosm experiments manipulating crayfish densities demonstrated a positive correlation between aggressiveness and foraging activity: crayfish were not only more interactive and aggressive towards conspecifics at higher densities, but also increased their foraging activity [66]. Such positive behavioral correlations are likely to be important in allowing crayfish to attain the densities needed to establish in, and dominate, invaded communities successfully.

Intraspecific variation in personality may also enhance post-establishment dispersal of invasive species. Cote and colleagues [33] found that mosquitofish were highly consistent in their behavioral tendencies. Moreover, boldness, activity level, exploratory behavior and sociability were all positively correlated. Importantly, personality traits affected dispersal tendencies, with asocial individuals dispersing further. More recently, Fogarty and colleagues [86] used a simulation model to highlight how personality-biased dispersal ability can facilitate the spread of invasive populations. Specifically, polymorphism in sociability increases the speed of the invasion front because the colonization of empty patches by asocial individuals helps facilitate the settlement of social types, which in turn induces faster dispersal of asocials at the invasion front.

Although it has yet to be tested empirically, intraspecific variation in behavioral traits may help explain how some introductions are able to transition across the full range of stages to become successful invaders [42]. However, although variation in key behavioral traits may enhance success at particular stages, the sequential selective nature of the introduction process may act to decrease behavioral variation as invasion progresses. It will therefore be important to consider the different selective pressures operating on individuals at each successive stage, as these will probably influence which individuals (and what personality types) are able to transition between stages. Future studies should focus on unintentional introductions to investigate the role of behavior in transition success throughout the entire introduction process.

species post-establishment. Thus, groups of correlated behaviors that enhance success across multiple introduction stages may represent an 'invasion syndrome' [42].

Although findings from recent research on mosquitofish [33,57–59,88] and crayfish [65,66,89] are strongly indicative of the existence of invasion syndromes in successful invaders, these studies have so far been limited to the latter stages of the introduction process (Box 1). The occurrence of invasion syndromes may explain why some species are repeatedly successful invaders, whereas others are repeated failures [42,67]. Although some behaviors that enhance success at one stage may be counterproductive at another, high levels of intraspecific variation in behavioral traits may enable successful invaders to transition successive stages of the introduction process. This idea is supported by a recent theoretical study that indicated that introduced species might spread more quickly when the population comprises individuals with a mix of personalities (i.e. behavioral polymorphism) rather than being behaviorally monomorphic [86]. These recent developments further emphasize that intraspecific variation in behavioral traits, and specific personalities or temperaments, have a role in determining invasion success in unintentional introductions.

Concluding remarks

The inability to link species-level traits consistently to invasiveness has led to an increasing tendency to invoke propagule pressure as the primary determinant of establishment success [5,13,14]. This paradigm is based on the simple premise that the 'more you introduce, the more you get' [15], yet it is incompatible with the observation that some species are repeated failures, despite being frequent stowaways [14,21,45,67]. A decade ago, a plea to consider the role of behavioral traits in species invasions [20] stimulated research into the behavior of invasive species and led to the important realization that intraspecific trait variation can enhance invasion success, often independent of propagule size [70]. Coupled with recent advances in understanding of animal personality and behavioral syndromes [42,85,87], inter- and intraspecific variation in behavior and other relevant traits (e.g. life-history and morphology), provide a clear mechanism with which to predict the success or failure of unintentional species introductions. However, the full potential of this approach has yet to be fulfilled, as most research has focused on the post-establishment stages of the introduction process. Adopting the framework outlined in this review, and an increased focus on the initial stages of the introduction process, should allow future research to investigate the role of behavior across each introduction stage and document the prevalence of invasion syndromes.

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