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# Don't neglect pre-establishment individual selection in deliberate introductions

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In a recent article in *TREE*, Chapple *et al.* [1] propose an individually-based framework that will greatly help to increase our understanding of invasion processes, thereby answering continuing calls for synthesis in this field [2]. They provide evidence that certain personality types are more likely to survive (they are 'selectively filtered') when transported out of their native range, and such selection might have long-lasting effects on establishment success and invasiveness. Chapple *et al.* explicitly target their thesis at unintentional introductions, arguing that "deliberate introductions essentially bypass the initial introduction stage" (i.e. the uptake, transport and release prior to establishment). Here we argue that selective pre-establishment filters should not be neglected for deliberate introductions: pre-establishment filters acting on individual variation likely provide key insight in invasion processes of any kind.

Deliberate introductions had their golden age when 'acclimatization societies' captured and shipped hundreds of alien species to European colonies. Such deliberate introductions were reduced when ecological and economic impacts of alien invasions became apparent, although new deliberate introduction pathways have progressively arisen. For example, millions of individuals from a variety of taxa are collected annually in the wild and traded internationally [3]. Those individuals that subsequently escape, or are released, constitute the primary seed of current invasions worldwide, e.g. [4,5]. Mortality during both historic [6] and more recent introductions is significant (e.g. for wild-caught birds, mortality estimates range within 7–62% between capture and acclimatization to captivity, 3–7% during international transport, 11–15% during quarantine, and up to 30% during the first months after quarantine [7]), implying that selection might change ('filter') the constitution of the original population throughout pre-establishment phases.

Individuals enter deliberate introduction pathways after being purposely captured from the wild. Evidence for personality-related sampling bias supports the notion that capture is often non-random, e.g. active or bold individuals are more likely captured than inactive or shy ones [8]. Trapped individuals would subsequently have to adapt to captivity, and locate and learn to use (novel) sources of food and water in highly unnatural circumstances (e.g. crowded cages). Under such challenging

scenarios, the more reactive, risk-averse, neophobic individuals might often refuse to eat or drink, causing considerable personality-related mortality both at initial storage but also after subsequent changes in location or holding conditions. Surviving individuals are likely subjected to further severe conditions during local and international transportation, storage, and quarantines, when they are often held at high densities, causing much and prolonged opportunity for overt aggressiveness among transported individuals. Stress at all these stages can modulate the individual's behavioral and physiological responses and decrease immunocompetence and condition of the more susceptible types. Individuals differ consistently in their physiological response to chronic stress [9], implying that selection likely acts on individual variation in stress physiology during those stages. Indeed, the reallocation and reintroduction literature provides ample evidence that capture of wild animals and successive handling, captivity and transportation cause cumulative acute and chronic stress which strongly compromises survival [10]. Finally, individuals must escape or be released to become introduced into a new range. During this stage, variability in behavior should again play a role since bolder, more active or more exploratory individuals are likely more prone to escape than others [11]. Moreover, shy or aggressive individuals are known to develop weak bonds with their owners [12], and unsatisfied buyers might thus release such types 'back into nature'. Thus, compared to the native population, the individuals that are ultimately introduced into a new environment likely represent a non-random sample with respect to activity, aggression and boldness.

In order to obtain a better understanding of current and past alien invasions, we encourage invasion biologists to consider selection on individual variation in personality during the pre-establishment stages of the invasion process, as well as indirect selection on life-history and physiological traits (e.g. life-span, dispersal potential and stress responses [9]). However, there is no reason to think that adopting such a framework isn't equally relevant for unintentional and deliberate introductions.

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# Intraspecific behavioral variation is important in both deliberate and unintentional species introductions: response to Carrete *et al.*

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In a recent review in *TREE* [1], we outlined a conceptual framework for how inter- and intraspecific behavioral variation may influence the success of unintentional species introductions, particularly during the pre-establishment phase of the introduction process [2]. Carrete and colleagues [3] argue that selective factors acting on intraspecific behavioral variation can also be important in the success of deliberate species introductions prior to establishment. We agree. Indeed, our review included several examples of how behavioral variability could enhance the post-establishment success of deliberately introduced species [4].

However, Carrete *et al.* imply that we did not consider individual-level behavioral variation to be important during the pre-establishment phase of deliberate species introductions. This is incorrect and appears to stem from a misinterpretation of several statements in our review relating to intentional species introductions bypassing the initial stages of the introduction process. We were simply highlighting, as have others [5–7], that the selection of species for intentional introduction is heavily influenced by human biases for species with particular traits or attributes (e.g. for biocontrol or the pet trade). That is, our statement related to the biased selection of species rather than to intraspecific behavioral variation.

Nonetheless, in the context of deliberate introductions, Carrete *et al.* outline several behaviors that may predispose certain individuals to capture, survival during transport and captivity, and release from captivity. Given that our review largely focused on unintentional species introductions, the behaviors highlighted by Carrete *et al.* provide an informative and valuable discussion that not only reinforces

one of our key points, that pre-establishment factors are important determinants of invasion success, but also broadens the application of our conceptual framework to both deliberate and unintentional species introductions.

Although pre-establishment factors may be important in the success of both types of species introduction, we argue that the selective pathways differ between deliberate and unintentional introductions. For deliberately introduced species, humans select the species that are introduced into new regions and, within these, selection acts on intraspecific behavioral variation (and variation in other traits) during capture, captivity, transport and release [3]. By contrast, unintentional introductions may be more reliant on biological factors, because interspecific trait and behavioral variation influences both the ‘opportunity’ and propensity of a species for transportation [1]. As outlined in our review, once ensnared in the transport vector, intraspecific behavioral variation may contribute to the likelihood of transitioning through the initial stages of the introduction process. However, despite these different pathways, important similarities in behaviors or personalities (e.g. boldness, exploratory behavior or aggression) could influence the success of both unintentional [1] and deliberate [3] introductions during the pre-establishment phase.

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