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How biological invasions affect animal behaviour: A global, cross-taxonomic analysis

Florian Ruland[1,2,3] | **Jonathan M. Jeschke**[1,2,3]

[1]Department of Biology, Chemistry, Pharmacy, Institute of Biology, Freie Universität Berlin, Berlin, Germany
[2]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany
[3]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

Correspondence
Florian Ruland
Email: florian.ruland@posteo.de

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Abstract

1. In the Anthropocene, species are faced with drastic challenges due to rapid, human-induced changes, such as habitat destruction, pollution and biological invasions. In the case of invasions, native species may change their behaviour to minimize the impacts they sustain from invasive species, and invaders may also adapt to the conditions in their new environment in order to survive and establish self-sustaining populations.
2. We aimed at giving an overview of which changes in behaviour are studied in invasions, and what is known about the types of behaviour that change, the underlying mechanisms and the speed of behavioural changes.
3. Based on a review of the literature, we identified 191 studies and 360 records (some studies reported multiple records) documenting behavioural changes caused by biological invasions in native (236 records from 148 species) or invasive (124 records from 50 species) animal species. This global dataset, which we make openly available, is not restricted to particular taxonomic groups.
4. We found a mild taxonomic bias in the literature towards mammals, birds and insects. In line with the enemy release hypothesis, native species changed their antipredator behaviour more frequently than invasive species. Rates of behavioural change were evenly distributed across taxa, but not across the types of behaviour.
5. Our findings may help to better understand the role of behaviour in biological invasions as well as temporal changes in both population densities and traits of invasive species, and of native species affected by them.

KEYWORDS
behavioural flexibility, biological invasions, ecological novelty, global change, HIREC, invasive alien species, phenotypic plasticity, temporal dynamics

1 | INTRODUCTION

Invasive species profoundly affect native species, communities and ecosystems (Bellard, Genovesi, & Jeschke, 2016; Vilà & Hulme, 2017). They are defined as species that have been intentionally or unintentionally (a) transported and (b) introduced to a new habitat by humans, where they have (c) established in the wild and (d) substantially spread beyond their point(s) of introduction (Blackburn et al., 2011; Jeschke, Keesing, & Ostfeld, 2013). Behaviour can affect all four of these steps of the invasion process. For example, ship rats *Rattus rattus* need to enter a ship and, after it has crossed the sea, leave it at a distant location. They may have

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to change their behaviour in this new location in order to find food, cope with potential competitors and evade predators and parasites, so that they are able to establish a population and spread there. Climatic conditions in the new environment may differ from those in the home range or fluctuate more strongly, triggering further behavioural adjustments.

Invasive species may be introduced to environments that are characterized by markedly different conditions compared to those in their native range. Entering a new ecosystem constitutes an environmental filter where individuals with compatible traits will be more likely to establish a viable population. The new abiotic and biotic conditions influence the varying mechanisms which enable behavioural change. For example, the golden apple snail *Pomacea canaliculata* is native to regions with a tropical climate. Upon its introduction to South Korea, it was subjected to selection for increased activity to reduce thermal stress (Bae, Chon, & Park, 2015). Native species may display behavioural changes associated with the arrival of an invasive species and the impacts it may have. The common planigale *Planigale maculata*, a native predator of Australia, has learned to avoid eating consuming the cane toad *Rhinella marina*, which is poisonous, over a few days of experiments with staged encounters (Llewelyn, Webb, Schwarzkopf, Alford, & Shine, 2010). In this example, the common planigale learned through individually acquired cues. Social learning (using the experience of others) can be safer, especially when ingesting potentially toxic prey, but this may fail if the environment changes too rapidly (Brown, 2012). Other mechanisms behind behavioural changes that were observed in invasions are epigenetics (Ardura, Zaiko, Morán, Planes, & Garcia-Vazquez, 2017) and maternal effects (Badyaev, 2005).

There is a difference in the potential for rapid genetic adaptation and the need for learning between native and invasive species. While the native species typically has a relatively large population size at the onset of the interaction, the invader may arrive to the new system in low numbers. Invasive species are therefore predicted to typically learn at the first two steps of the invasion process; the adaptive flexibility hypothesis predicts an innovation to appear through individual learning in the early stages of invasion and to then disperse across the population via social learning (Wright, Eberhard, Hobson, Avery, & Russello, 2010). Generation time and the number of reproductive events differ vastly among taxa, as do fecundity and parental care. Investment in learning and the potential for selection to act will therefore differ among taxa. Understanding this taxonomic range of behavioural changes and their underlying mechanisms thus requires comparisons across taxonomic groups (Griffin, 2016).

Knowing the speed of behavioural change is important for predicting lags in invader impacts (Epanchin-Niell & Liebhold, 2015) and potential boom-bust dynamics (Strayer et al., 2017; Strayer, Eviner, Jeschke, & Pace, 2006 and references therein). The difference between an immediate and a delayed behavioural change may be especially important in novel ecological settings when species that have not previously interacted come into contact (cf. Saul & Jeschke, 2015). Differences in the speed of behavioural change between invasive and native species might explain some population dynamics in invaded systems. On the one hand, if a delayed behavioural innovation allows an invasive species to feed on an abundant prey species in its new environment, this will likely lead to a delayed increase in the population density of the invasive species. On the other hand, a delayed innovation in a native species allowing it to effectively reduce predation by an invader may reduce the invader's population density with a time delay. Similarly, the recognition of the invader as prey can lead to an increase in native species and increased predation pressure on the invader. This effect was observed in the Jeziorsko Reservoir in central Poland, where native mute swans *Cygnus olor* started to feed on invasive zebra mussels *Dreissena polymorpha*. Swans began to exploit zebra mussels as a food source in the winter 1998/1999, when the mussels became abundant a few years after their introduction (Wlodarczyk & Janiszewski, 2014). Whether the population of a high-impact invader will crash without targeted management action is of high practical value, but at the moment we cannot predict which native or invasive species will change their behaviour quickly, with a delay or not at all.

Behavioural changes in dynamic environments are generally well-investigated (Wong & Candolin, 2015), and biological invasions have been recognized as the drivers of behavioural change (Holway & Suarez, 1999). However, the scope of studies investigating the role of behaviour in biological invasions is usually limited to either invasive or native species. For invasive species, some studies found certain personality traits like activity or boldness (Brodin & Drotz, 2014) and behavioural flexibility (Sol & Lefebvre, 2000; Weis & Sol, 2016) to be related to invasion success. Behavioural flexibility was also found to be beneficial to native species interacting with invaders (Berthon, 2015; Sih, Trimmer, & Ehlman, 2016). Other studies have explored the evolutionary capacity of native species responding to invasion (Strauss, Lau, & Carroll, 2006), the naiveté of natives towards invaders (Carthey & Banks, 2014) and (along similar lines) the danger of evolutionary traps in interactions with invaders (Robertson, Rehage, & Sih, 2013). Investigations with a behavioural focus have proposed concepts about the specific mechanisms underlying behavioural change in both native (Berthon, 2015) and invasive species (Wagner, 2017), but not both in parallel. Most studies of behavioural changes caused by invasions focus on foraging and dispersal, some on mating and competition and a few on anti-predator behaviour (Berger-Tal et al., 2016).

We are not aware of a synthesis that combines data on behavioural changes in invasive and native species across taxonomic groups, the types of behaviour, the underlying mechanisms and the speed of change. We therefore aimed to achieve such a synthesis, bridging research in invasion biology, conservation and animal behaviour across taxonomic groups. While we recognize a growing literature on plant behaviour (Trewavas, 2014), we restrict our study to animal behaviour.

The following research questions were addressed in this study: (a) Do different types of behaviour change in native as compared to invasive species? (b) Do some types of behaviour change faster than others? (c) Is learning more commonly studied in vertebrates than invertebrates (Rosenthal, Gertler, Hamilton, Prasad, & Andrade, 2017)?

(d) Are specific types of behavioural change associated with specific underlying mechanisms? In all these comparisons, we distinguish between invasive and native species, as they are subjected to very different ecological settings, and we consider potential biases in published studies, especially towards high-impact invaders.

2 | MATERIALS AND METHODS

2.1 | Literature search

We followed the recommendations for literature search by the PRISMA statement for meta-analyses (Moher, Liberati, Tetzlaff, & Altman, 2009). Specifically, we searched the Web of Science (on 30 June 2015 from the institution Freie Universität Berlin in Germany). We searched "All databases", but selected the research areas "Behavioural Sciences", "Genetics Heredity", "Environmental Sciences Ecology", "Plant Sciences", "Biodiversity Conservation", "Zoology" and "Evolutionary Biology". We used the following general search string: Behavio* AND (shift* OR change* OR transition*) AND (alien OR exotic OR introduc* OR invas* OR naturali?ed OR nonindigenous OR non-indigenous OR nonnative OR non-native).

This initial search yielded 6,463 studies before and 5,948 studies after duplicate removal (see Supporting Information Appendix S1 for PRISMA flow chart). We then scanned the titles and abstracts of these studies to exclude those that did not focus on behavioural change. We reviewed the remaining 524 studies to identify those that fit our criteria of eligibility: (a) one or more specific behaviours were observed to have changed; (b) the change in behaviour had to be observed either in an invasive species or in a native species now interacting with an invasive species. We defined behaviour as 'the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes' (Levitis, Lidicker, & Freund, 2009, p. 103). We found 191 studies from 1990 to 2015 that were eligible according to these criteria. The unit of observation in our study is the individual record of behavioural change, of which there were 360 in total. Some studies documented more than one record of a species' behavioural change or different types of behaviour that changed for one species.

2.2 | Data on individual records of behavioural change

2.2.1 | General data

Each record documented the behavioural change(s) of one native or invasive species. We extracted the following information for each record:

- background information (year of publication, title, journal and location of study),
- type of study (laboratory, field or enclosure),
- type of evidence (experimental or observational/correlational),
- type of habitat (aquatic, terrestrial, marine or any combination),
- focal species, classified as (a) native or invasive and (b) by taxonomic group, using five vertebrate groups (mammals, birds, reptiles, amphibians and fish) and four invertebrate groups (insects, crustaceans, molluscs and other invertebrates) and
- species that the focal species interacted with (if any).

2.2.2 | Types of behaviour

While most studies that compare drivers and taxonomic bias in behavioural shifts focus on feeding innovations, for example a shift of prey items or technical innovations (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005), we aimed to capture the full range of behaviours that can change during invasions in native or invasive species. We noted the observation unit of behavioural change in each record, for example gut content analysis showing that a predator species ingested a new prey species. The act of predating on a new species, potentially using a new technique, is an example of the *means* of the animal species to change its ecological interaction with the environment.

As we were more interested in the ecological context of the behaviour and not the actual motor activity performed, we then classified the *ends* of the behavioural shift using one of the following six, mutually exclusive categories: (a) Feeding (behavioural changes associated with feeding); (b) Defence (behavioural changes associated with defence against a predator or parasite); (c) Abiotic (behavioural changes to better cope with abiotic stress); (d) Dispersal (behavioural changes enabling better dispersal or migration); (e) Mating (behavioural changes enabling reproduction, including courtship) and (f) Competition (behavioural changes to better cope with a directly interacting competitor, i.e. in interference competition). For example, the Hawaiian Oahu Elepaio *Chasiempis ibidis* move their nests to higher trees as a defence against nest predation by black rats *R. rattus* (Vanderwerf, 2012): this behavioural change was classified as a 'Defence'. Four of the 360 records of behavioural change could not be classified using one of the above categories: these records were excluded from the analyses using the type of behaviour.

2.2.3 | Speed of behavioural change

Some records in our dataset were reported to be instant, flexible behavioural changes, whereas others were plastic changes over an individual's lifetime or adaptations over generations. In the first step, we differentiated between those cases of behavioural change that happened instantly and those that did not. We noted an *instant* change if this was indicated by the authors of the original study. The native Australian whelk *Haustrum vinosum*, for example, recognizes predator cues from the invasive European green crab *Carcinus maenas* independently if the crab was present 0, 20 or 100 years at the site (Freeman, Wright, Hewitt, Campbell, & Szeto, 2013).

For behavioural changes that did not happen instantly, the speed of change and the underlying data varied vastly. In some studies, sites with different, known invasion histories were compared, such as for native fence lizards *Sceloporus undulatus* in the southern United States predated by the invasive red imported fire ant *Solenopsis invicta*. The anti-predator response of the lizards was compared between uninvaded sites and sites invaded 23, 54 and 68 years prior to the data collection (Langkilde, 2009). In other cases, species that have never interacted in the wild were experimentally brought together, like the native European mirid bug *Macrolophus pygmaeus* feeding on the invasive tomato leafminer *Tuta absoluta* in a laboratory setting (Jaworski, Bompard, Genies, Amiens-Desneux, & Desneux, 2013). If available, we also noted the point in time when the species started to spread in the introduced range and thus interactions with the native species started to become far more common. An example for this scenario is the more frequent egg rejection of native village weavers *Ploceus cucullatus* in Hispaniola in the West Indies with a growing population of invasive shiny cowbirds *Molothrus bonariensis* documented over the course of 16 years (Robert & Sorci, 1999). In some cases, it was appropriate to use the difference between the time of introduction and the first documentation of the behavioural change. While this time span can be very long, as for example in case of the introductions of several mammal species to Australia with the first Europeans, we only used this time span if the author(s) gave evidence for the respective behaviour changing over that time span, for example comparisons between different sites.

We used the categorical data of instant (i.e. flexible) versus non-instant (e.g. plastic or adaptive) behavioural changes to compare the speed of changes across different types of behaviour, native and invasive species, and between our five vertebrate and four invertebrate groups, using chi-squared tests with 100,000 simulations. The data on the more precise speed of change were used to test if the mechanisms described in the following paragraphs match their predicted speeds. For these analyses, we only used the time records of behavioural change where there was evidence of the change happening over a known interaction time as described in the previous two paragraphs. The results of these analyses are provided in Supporting Information Appendix S1.

2.2.4 | Mechanisms of behavioural change

Another goal of this study was to document the different mechanisms of behavioural change, to compare their speed of change and to look at their distribution across taxa. In order to categorize all mechanisms behind behavioural changes in our dataset, we followed an explorative approach. We noted down each mechanism of behavioural change proposed by the author(s), as in many cases more than one mechanism was mentioned. In the next step, we checked if the author(s) provided empirical evidence for the specific mechanism or if it was a speculation without such evidence. Both types of information are provided in our dataset (see Supporting Information S2), but only mechanisms with empirical evidence were analysed in this study.

Only few studies reported epigenetic or maternal effects (but see Liebl & Martin, 2014, or Forister et al., 2013 respectively). Therefore, we restricted our analyses to two types of mechanisms that were commonly reported: rapid genetic adaptation and learning. A record of genetic adaptation was noted if it was documented that a behavioural change during the invasion of a species was based on a genetic change. This happened, for example, in the Polynesian field cricket *Teleogryllus oceanicus*, where the flatwing morphology is more common in males in the invaded range (Oceanic islands like Kauai [Hawaii] have up to 90% flatwing males) as compared to the native range. This mutation disables courtship songs, but renders males less susceptible to the acoustically oriented parasitoid fly *Ormia ochracea*. As most males consequently do not perform courtship songs in the invaded range, females have evolved relaxed mating requirements there (Tinghitella & Zuk, 2009). We noted a behavioural change through learning if the change occurred after (and not before) the interaction with the stimulus, either directly by the focal individual or through observation of or communication with conspecifics. The soft-shell clam *Mya arenaria*, for example, changed its burrowing behaviour in the presence of the invasive European shore crab. In this particular case, social cues from impacted conspecifics were sufficient to increase burrowing depth (Flynn & Smee, 2010).

We tested the assumption that learning occurs faster than genetic adaptation, both in absolute and relative time, by calculating Hedge's g effect sizes (see Supporting Information Appendix S1 for details). Then, we compared the distribution of these two mechanisms both across invasive and native species, and across taxonomic groups and types of behaviour (Sections 3.3. and 3.4 of this paper respectively).

2.3 | Weighting records in the database

To correct for potential biases that arise with multiple records in one study, we analysed both weighted and unweighted data. Following previous studies (e.g. Heger & Jeschke, 2014; Willer, Li, & Abecasis, 2010; Zaykin, 2011), the relative weight of a record was calculated as 1/sqrt(number of records in the study), so that the combined weight of all records in one study was sqrt(number of records in the study). Since there were no qualitative differences in the results between weighted and unweighted data, we chose to present the results for unweighted data in the main article for higher accessibility, while those for the weighted analyses are provided in the Supporting Information Appendix S1.

All analyses were conducted using the CORE package of R (version 3.4.4, R Core Team, 2018) and the package EFFSIZE (Torchiano, 2020). Pyramid plots in Figures 1, 4 and 5 were created with the use of the package PLOTRIX (Lemon, 2006).

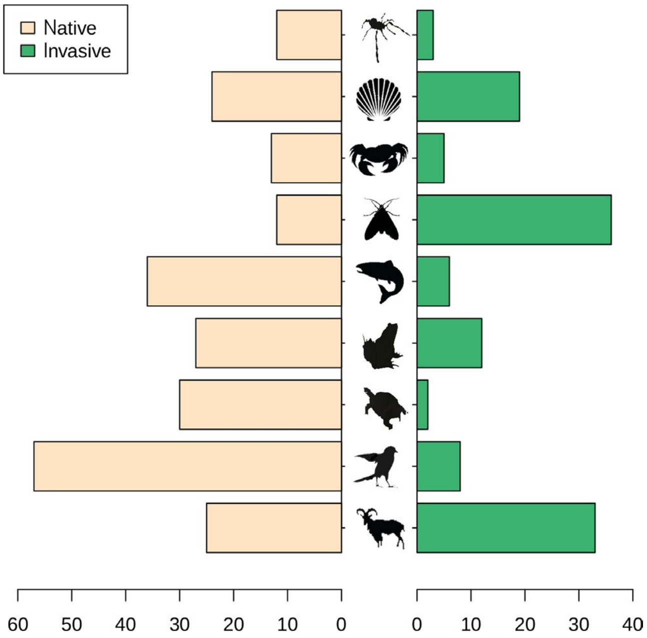

FIGURE 1 Cases of behavioural change across taxonomic groups in native versus invasive species

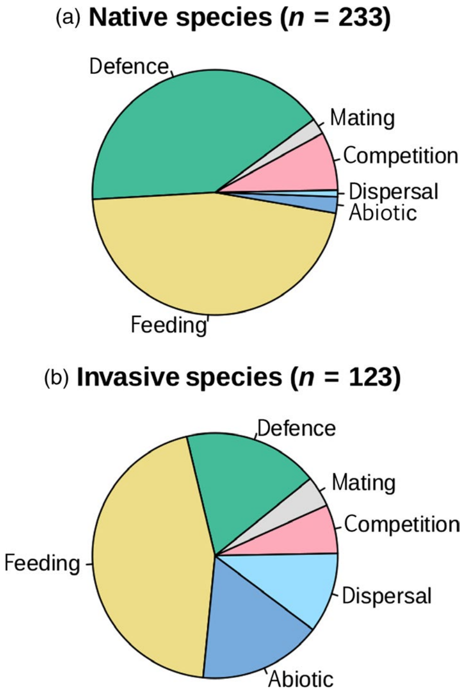

FIGURE 2 Types of behaviour across (a) native and (b) invasive species (*n* refers to the number of records)

3 | RESULTS

We will present our results in the same order as the questions outlined in the Introduction. First, however, we look at potential biases in the dataset. Out of the 360 records of behavioural change in total, birds were most frequently studied (65 records), followed by mammals (58 records) and insects (48 records). This is a comparatively small bias compared to the field of behavioural ecology in general, where most studies are focused on species that are relatively closely related or appealing to humans or show supposedly complex behavioural patterns, that is, mammals and birds. For example, Rosenthal et al. (2017) reported that about half of the studies published in the journal *Animal Behaviour* from 1953 to 2015 focused on mammals and birds. Our sample is less taxonomically biased towards mammals and birds, as about two thirds of the records of behavioural change we found were documented in the remaining taxa reptiles, amphibians, fish and invertebrates. Interestingly, our dataset indicates that different taxa were primarily investigated for invasive versus native species: we found many studies on invasive mammals and insects, whereas the relative majority of studies looking at native species focused on birds, with significant numbers also for fish, mammals and molluscs (Figure 1). Across all 360 records of behavioural change, only 15 species appeared in four or more records; six of these are included in the '100 of the World's Worst Invasive Alien Species' list of IUCN's Global Invasive Species Database (www.iucngisd.org/gisd/100_worst.php): the black rat *R. rattus*, cane toad *R. marina*, zebra mussel *D. polymorpha*, golden apple snail *P. canaliculata*, feral pig *Sus scrofa* and Argentine ant *Linepithema humile*. In conclusion, while the mild taxonomic bias towards mammals and birds (see Figure 1) should be kept in mind when interpreting the results of our cross-taxonomic analyses, the results reported in the following sections are not primarily driven by observations from a few species, but draw from a large number of taxonomic groups.

3.1 | Different behavioural changes reported for native and invasive species

We found different types of behaviour changing in native versus invasive species (Figure 2; chi-squared test, 100,000 bootstrap simulations with the numbers of records across natives and invasives across the six categories; $\chi^2 = 54.95$, $p < 0.001$). In particular, changes to defence behaviour (avoiding predation or parasitism) were more commonly reported in native species when compared with than invasive species (Figure 2). These native species include marsupials impacted by the cane toad invasion in Australia (Llewelyn et al., 2010), the Eastern fence lizard impacted by invasive ants in the United States (Langkilde, 2009) and the common toad *Bufo bufo* impacted by invasive Turkish crayfish *Astacus leptodactylus* in France (Mandrillon & Saglio, 2007).

3.2 | Specific types of behaviour change at different speeds

The speed of behavioural change varied substantially across these different categories of behaviour (Figure 3). We found the most records of instant changes for coping strategies are associated with abiotic factors (climatic conditions, oxygen levels in the water, hydration in terrestrial habitats; Figure 3). While changes

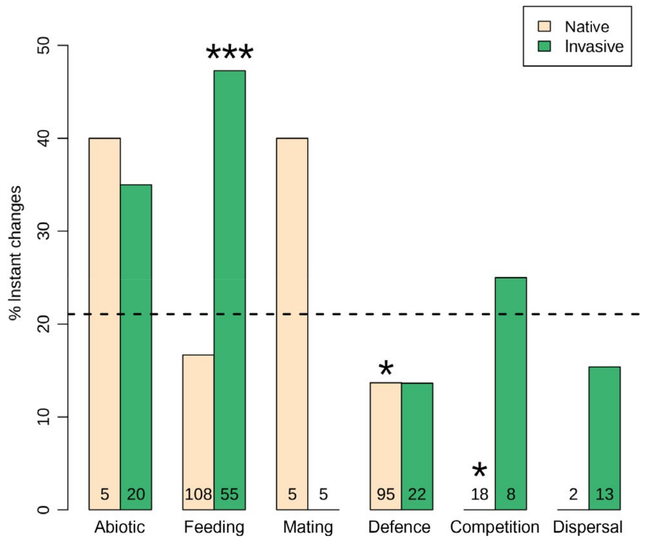

FIGURE 3 Percentage of records of behavioural change that happened instantly across types of behaviour in native and invasive species. The numbers of records in each category is given at the bottom of each bar. Significant differences from the mean (shown as dashed line) are indicated above bars (*$p < 0.05$, ***$p < 0.001$)

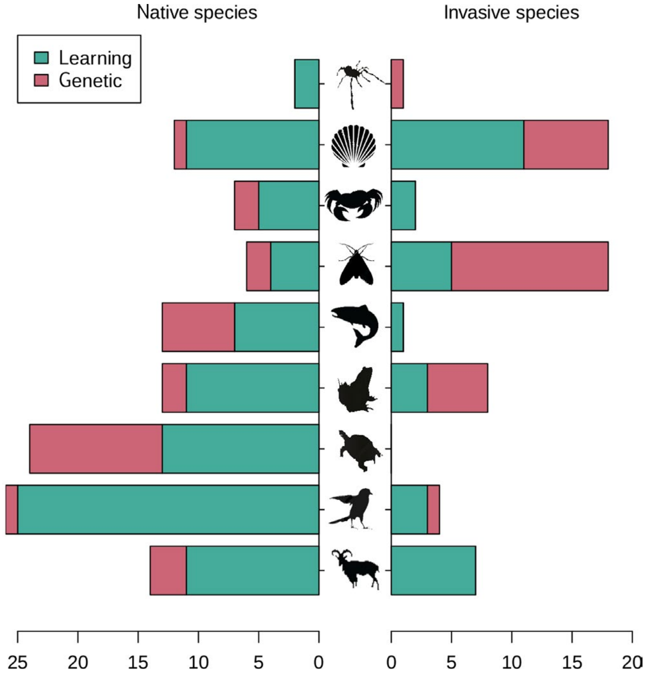

FIGURE 4 Cases of behavioural change through learning or rapid genetic adaptation across taxonomic groups in native versus invasive species

to abiotic conditions usually develop over long time periods, a species introduced to new environments will experience different abiotic conditions immediately. For example, in its invasive range, the green mussel *Perna viridis* rapidly closes its valves in waters with low salinity in order to survive osmotic stress (McFarland, Donaghy, & Volety, 2013). Similarly, native species that have been pushed out of their optimal abiotic niche through predation, competition or habitat alteration have to cope with the new abiotic conditions instantly (Stellatelli, Vega, Block, & Cruz, 2013).

3.3 | Mechanisms enable change at different speeds

Studies indicate that learning allows for faster behavioural change than genetic evolution (Zuk, Bastiaans, Langkilde, & Swanger, 2014). Our results support this finding, both in absolute terms as well as when corrected by age at sexual maturity (see Supporting Information Appendix S1). Across taxonomic groups, species changed their behaviour at least to some degree through both learning and rapid genetic adaptation (Figure 4). We expected a taxonomic bias, whereby learning would be more commonly reported for vertebrate than invertebrate species, as studies on learning tend to traditionally focus on mammals and birds (Avital & Jablonka, 2000). However, this was not the case (chi-squared test with 100,000 bootstrap simulations: $\chi^2 = 3.26$, $p = 0.09$). Indeed, we found reports for several learning experiments involving invertebrates. Only when specifically comparing the nine taxonomic groups in our dataset (five vertebrate and four invertebrate groups) did we find differences, as insects were frequently reported to show rapid genetic adaptation, whereas birds were most commonly documented to learn (chi-squared test with 100,000 bootstrap simulations: $\chi^2 = 26.1$, $p < 0.001$).

TABLE 1 Numbers of records of behavioural change in native and invasive species that happened instantly or not

	Native species	Invasive species
Instant changes	35	40
Non-instant changes	201	84

Native species changed their behaviour more frequently through learning than invasive species, which was not exclusively explained by the mild taxonomic bias in our dataset (chi-squared test with 100,000 bootstrap simulations: $\chi^2 = 8.7$, $p < 0.01$). In the most represented taxonomic groups of our invasive species sample (insects, molluscs and amphibians), the ratio of rapid genetic adaptation to learning was higher than for native species from these groups. A possible explanation is high selection pressure in the invaded range coupled with relatively high propagule pressure for these taxa.

There were fewer confirmed cases of behavioural changes through learning as opposed to rapid genetic evolution in invasive than native species (Figure 4), which is counter-intuitive when considering the difference in speed of change between these mechanisms (learning being faster than genetic evolution). This might be a methodological issue though, as instant behavioural changes are more common in invasive than native species (chi-squared test with 100,000 bootstrap simulations: $\chi^2 = 14.97$, $p < 0.001$, see Table 1). While some of these instant changes are due to

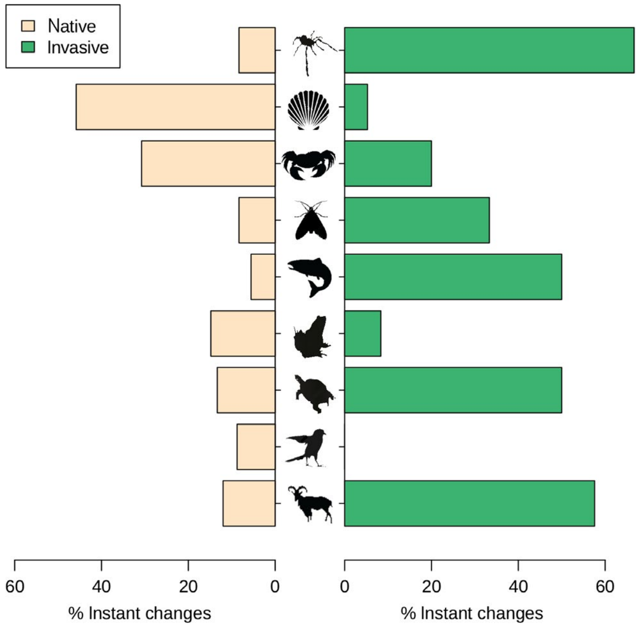

FIGURE 5 Percentage of behavioural changes that happened instantly across taxa in native versus invasive species

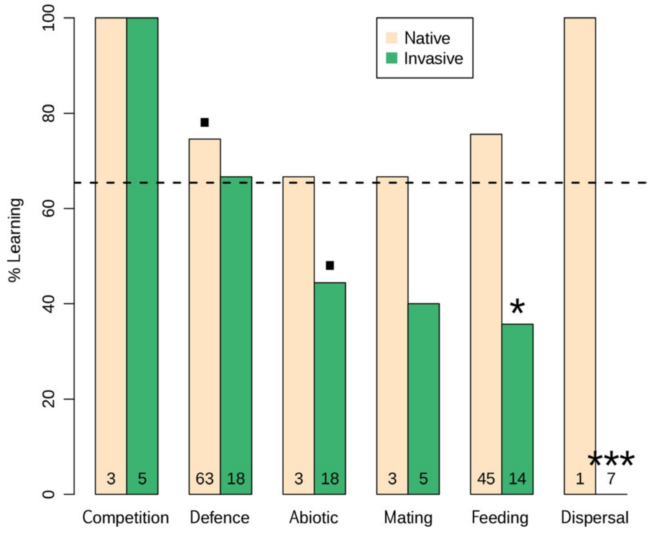

FIGURE 6 Percentages of behavioural change through learning (as compared to rapid genetic adaptation) across types of behaviour in native versus invasive species. The dashed line indicates the mean percentage across all records. Sample sizes are indicated at the bottom of the bars. Significant differences from the mean are indicated above bars (■$p < 0.1$, *$p < 0.05$, ***$p < 0.001$)

learning, we do not know which ones if such information was not provided by the authors. Other instant changes are facilitated by pre-disposition towards the new behaviour, which are latent traits that accelerate behavioural shifts and allow for behavioural flexibility (Wagner, 2017).

We found significant differences in the speed of behavioural change across taxonomic groups (Figure 5, chi-squared test with 100,000 bootstrap simulations, $\chi^2 = 24.13$, $p < 0.001$). Learning was not evenly distributed across taxa, thus we expected this corresponding difference in the speed of change. There was no difference in the frequency of instant changes between vertebrates and invertebrates (chi-squared test with 100,000 bootstrap simulations: $\chi^2 = 3.8$, $p = 0.06$). Results from the analysis with weighted records were similar (see Supporting Information Appendix S1).

3.4 | Specific types of behavioural change are associated with specific mechanisms

We found evidence for the mechanisms of behavioural change to differ across types of behaviour (Figure 6). Among invasive species, dispersal was most strongly associated with genetic adaptation, followed by feeding, coping with abiotic environmental differences and mating. Across types of behaviour, learning was more common in native than in invasive species and most pronounced in defence behaviour, although not significantly so. It may be more challenging to recognize and behaviourally adapt to a new threat in the form of a predator or parasite than to adapt to a change in temperature. Threat cues from novel predators require interpretation before an appropriate response can be performed, which can be rather complex (York & Bartol, 2016). Also, the predator may plastically respond to the new defence behaviour, making further changes by the defender necessary.

4 | DISCUSSION

This study represents a general, cross-taxonomic overview of behavioural changes caused by biological invasions, considering both native and invasive species and a wide range of different data. We found that some taxonomic groups, particularly mammals and birds, are more frequently investigated than other taxa. However, this taxonomic bias was relatively mild overall.

Behavioural changes to avoid enemies have been more frequently reported for native than invasive species. This finding is in line with previous studies based on smaller sample sizes (Berthon, 2015; Strauss et al., 2006). It also provides potential support for the enemy release hypothesis which posits that the absence of enemies in the exotic range of invasive species is a cause of invasion success (Heger & Jeschke, 2014, 2018; Keane & Crawley, 2002). A more specific variant of this hypothesis states that 'invaders are released from enemies', which is empirically better supported than the enemy release hypothesis in general (Heger & Jeschke, 2018).

Behavioural changes that were less frequently observed in invasive than native species were defence measures against predation or parasitism. A possible underlying reason is the lower risk of invaders to be attacked by resident predators that lack a joint evolutionary history with such potential prey. An alternative explanation may be a research bias, whereby study results are influenced by the classic image of an invasive species as a damaging new predator, while native species are viewed as those under threat. Similarly, there may be little concern regarding the fate of invasive species (they are not often listed as threatened on the IUCN Red List, particularly in comparison to the native species they impact), and thus the predation impacts they sustain may not be recorded. However, the role of invasive prey's anti-predator behaviour in invasions is increasingly being recognized (Mennen & Laskowski, 2018).

Changes associated with dispersal behaviour and coping with the abiotic environment were more frequently reported for invasive than native species. Behavioural traits linked to dispersal were expected to have changed more often in invasive species, as dispersal and spread are part of the invasion process, particularly if a non-native species is to thrive. For example, cane toads were found to move faster and follow straighter paths following selection in their new environment, the open Australian landscape (Brown, Phillips, & Shine, 2014; see also Kelehear & Shine, 2020). Environmental conditions in new habitats can be challenging for invasive species, requiring changes in activity, movements or strategies against dehydration. Invasive species commonly have different environmental characteristics in the invaded range to cope with, but also native species can be forced to change their behaviour due to invasions. For example, the native sand lizard species *Liolaemus wiegmannii* changed its basking pattern after the spread of acacia trees *Acacia longifolia* in Argentina, which produce significantly more shade than the native vegetation (Block, Stellatelli, García, Vega, & Isacch, 2013).

More studies on rapid changes to feeding behaviour were available for invasive than for native species (Figure 3). Indeed, there is a large and still growing body of research showing how dietary flexibility explains invasion success (Sol & Lefebvre, 2000; Wright et al., 2010). We may therefore find more studies on invasive species exhibiting rapid dietary behavioural changes because they are the ones to persist, and therefore to go on to have impacts and be studied, in new environments (see Evans, Pigot, Kumschick, Şekercioğlu, & Blackburn, 2018). The field of innovation research quantifies the innovation in a new behaviour of a species. In birds in particular, this literature distinguishes between simple 'food type innovations' and more complex 'technical innovations' (Ducatez, Clavel, & Lefebvre, 2014; Overington et al., 2009). It is often not the greater innovation propensity of invaders, but simply the choice of a new food source without the accompanying behavioural innovation that facilitate invasions.

On the other side, forming defence or escape strategies against new predators or parasites are relatively slow processes, both for invasive and native species (Figure 3; see also Anton, Geraldi, Ricciardi, & Dick, 2020). There were more records of this kind of behavioural change in native species when compared to invasive species. Thus, impacts to native species may be severe where invasive species with high levels of dietary flexibility interact with native species with slow behavioural responses to predation. We believe that both factors—native versus non-native origin as well as type of behaviour—contribute to this effect, as changes in feeding behaviour were significantly faster in invasive than in native species, whereas changes in defence behaviour against novel predators were slow for both native and invasive species.

The situation for native species is further aggravated as the change in the defence behaviour might not even be effective (Carthey & Banks, 2014). Following the proposed definitions of Banks and Dickman (2007), there are three levels of naiveté. First, most harmful to the respective species is level-1 naiveté where the prey does not recognize the predator as a potential threat. In level-2 naiveté, the prey species recognizes the danger, but the reaction is inappropriate as an anti-predator response. Finally, if the prey shows level-3 naiveté, it manages to recognize the potential threat and shows an appropriate response, but it is not skilled enough to escape. For example, Australian bilbies *Macrotis lagotis* were trained to recognize and avoid introduced predatory feral cats *Felis catus* and foxes *Vulpes vulpes*, but survival rates after release into the wild did not improve significantly (Moseby, Cameron, & Crisp, 2012). The bilbies were trained to show the appropriate response, which is leaving the burrow when smelling the scent of the predator, but it was still ineffective, therefore showing level-3 naiveté. We describe only the speed of behavioural changes in native or invaders and do not have data on their population dynamics outcomes. However, we can say that not changing the behaviour instantly (therefore staying in the most harmful level-1 or level-2 naiveté) is happening more commonly for native than invasive prey species. We then analysed how underlying mechanisms that allow for faster or slower changes are distributed across native and invasive species, and across taxonomic groups.

Furthermore, we showed that different types of behaviour change at different speeds. For example, and worryingly from the perspective of native species, feeding-related behavioural changes were faster in invasive species than changes in avoidance behaviour against predators and parasites in native (and invasive) species (the latter type of behavioural change was more prevalent among natives). Thus, if our findings are not mainly driven by a bias in the available literature, they suggest a disadvantage in the arms race between invasive predators and native prey. This may in part explain the cases of boom-bust population dynamics of predator invaders, which swiftly shift to new prey in their exotic range (leading to a 'boom'), but decrease in their abundance ('bust') when their prey eventually develop avoidance strategies or have become (locally) extinct.

These differences in the speed of behavioural changes are enabled by different mechanisms. For instance, the mechanism underlying a change in defence behaviour of prey against predators was typically learning. It seems that at least for the cases of biological invasions covered by the studies analysed here (either introduced predators interacting with resident prey, or resident predators interacting with introduced prey), predators frequently have an advantage due to a high level of eco-evolutionary experience (sensu Saul & Jeschke, 2015) in these interactions. This means for introduced predators that they have interacted with, and predated upon, similar prey species in their native range; while the resident prey species sustaining impacts often have no prior experience with such predators (and analogously for resident predators interacting with introduced prey). This higher eco-evolutionary experience relates to a higher frequency of pre-dispositions in predators as compared to prey species. Whether this result is robust for cases of biological invasions beyond those covered in our dataset is a question to be addressed in the future.

We publish our dataset of 360 records extracted from 191 papers along with this study to provide a resource for additional analyses and encourage other scientists to expand it. The dataset allows for several analyses that we could not focus on here, for example in-depth analyses for particular taxonomic groups. To foster the investigation of mechanisms underlying behavioural change, we also suggest that future empirical studies include targeted observations or experiments focusing on such mechanisms. Behaviour and, more specifically, behavioural changes have only been recently recognized as shaping outcomes of biological invasions (Weis & Sol, 2016). As pointed out above, these shifts can be of high interest for other research fields, such as animal learning, innovation and conservation biology. We hope to inspire more research in that direction to: (a) help predict how changes in invader behaviour affect communities and ecosystems; (b) protect native species by assisting their behavioural change and (c) draw general conclusions on the role of behaviour and its temporal dynamics for biological invasions.

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AUTHORS' CONTRIBUTIONS

F.R. and J.M.J. conceived the ideas and designed methodology; F.R. collected and analysed the data and led the writing of the manuscript; J.M.J. contributed critically to the drafts.

DATA AVAILABILITY STATEMENT

Data are archived in Dryad Digital Repository https://doi.org/10.5061/dryad.573n5tb56 (Ruland & Jeschke, 2020).

ORCID

Florian Ruland https://orcid.org/0000-0002-5785-1733
Jonathan M. Jeschke https://orcid.org/0000-0003-3328-4217

REFERENCES

Anton, A., Geraldi, N. R., Ricciardi, A., & Dick, T. A. (2020). Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B: Biological Sciences*, *87*, 20192978. https://doi.org/10.1098/rspb.2019.2978

Ardura, A., Zaiko, A., Morán, P., Planes, S., & Garcia-Vazquez, E. (2017). Epigenetic signatures of invasive status in populations of marine invertebrates. *Scientific Reports*, *7*, 1–10. https://doi.org/10.1038/srep42193

Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge, UK: Cambridge University Press.

Badyaev, A. V. (2005). Maternal inheritance and rapid evolution of sexual size dimorphism: Passive effects or active strategies? *The American Naturalist*, *166*, 17–30. https://doi.org/10.1086/444601

Bae, M. J., Chon, T. S., & Park, Y. S. (2015). Modeling behavior control of golden apple snails at different temperatures. *Ecological Modelling*, *306*, 86–94. https://doi.org/10.1016/j.ecolmodel.2014.10.020

Banks, P. B., & Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution*, *22*, 229–230. https://doi.org/10.1016/j.tree.2007.02.006

Bellard, C., Genovesi, P., & Jeschke, J. M. (2016). Global patterns in threats to vertebrates by biological invasions. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 220152454. https://doi.org/10.1098/rspb.2015.2454

Berger-Tal, O., Blumstein, D. T., Carroll, S., Fisher, R. N., Mesnick, S. L., Owen, M. A., … Swaisgood, R. R. (2016). A systematic survey of the integration of animal behavior into conservation. *Conservation Biology*, *30*, 744–753. https://doi.org/10.1111/cobi.12654

Berthon, K. (2015). How do native species respond to invaders? Mechanistic and trait-based perspectives. *Biological Invasions*, *17*, 2199–2211. https://doi.org/10.1007/s10530-015-0874-7

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., … Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, *26*(7), 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Block, C., Stellatelli, O. A., García, G. O., Vega, L. E., & Isacch, J. P. (2013). Factors affecting the thermal behavior of the sand lizard *Liolaemus wiegmannii* in natural and modified grasslands of temperate coastal dunes from Argentina. *Journal of Thermal Biology*, *38*, 560–569. https://doi.org/10.1016/j.jtherbio.2013.09.009

Brodin, T., & Drotz, M. K. (2014). Individual variation in dispersal associated behavioral traits of the invasive Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1854) during initial invasion of Lake Vänern, Sweden. *Current Zoology*, *60*, 410–416. https://doi.org/10.1093/czoolo/60.3.410

Brown, C. (2012). Experience and learning in changing environments. In U. Candolin & B. Wong (Eds.), *Behavioural responses to a changing world: Mechanisms and consequences* (pp. 46–60). Oxford University Press. https://doi.org/10.1093/acprof:osobl/9780199602568.003.0004

Brown, G. P., Phillips, B. L., & Shine, R. (2014). The straight and narrow path: The evolution of straight-line dispersal at a cane toad invasion front. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20141385. https://doi.org/10.1098/rspb.2014.1385

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, *89*, 932–949. https://doi.org/10.1111/brv.12087

Ducatez, S., Clavel, J., & Lefebvre, L. (2014). Ecological generalism and behavioural innovation in birds: Technical intelligence or the simple incorporation of new foods? *Journal of Animal Ecology*, *84*, 79–89. https://doi.org/10.1111/1365-2656.12255

Epanchin-Niell, R. S., & Liebhold, A. M. (2015). Benefits of invasion prevention: Effect of time lags, spread rates, and damage persistence. *Ecological Economics*, *116*, 146–153. https://doi.org/10.1016/j.ecolecon.2015.04.014

Evans, T., Pigot, A., Kumschick, S., Şekercioğlu, Ç. H., & Blackburn, T. M. (2018). Determinants of data deficiency in the impacts of alien bird species. *Ecography*, *41*, 1401–1410. https://doi.org/10.1111/ecog.03232

Flynn, A. M., & Smee, D. L. (2010). Behavioral plasticity of the soft-shell clam, *Mya arenaria* (L.), in the presence of predators increases survival in the field. *Journal of Experimental Marine Biology and Ecology*, *383*, 32–38. https://doi.org/10.1016/j.jembe.2009.10.017

Forister, M. L., Scholl, C. F., Jahner, J. P., Wilson, J. S., Fordyce, J. A., Gompert, Z., … Nice, C. C. (2013). Specificity, rank preference, and the colonization of a non-native host plant by the Melissa blue butterfly. *Oecologia*, *172*, 177–188. https://doi.org/10.1007/s00442-012-2476-8

Freeman, A. S., Wright, J. T., Hewitt, C. L., Campbell, M. L., & Szeto, K. (2013). A gastropod's induced behavioral and morphological responses to invasive *Carcinus maenas* in Australia indicate a lack of novelty advantage. *Biological Invasions*, *15*, 1795–1805. https://doi.org/10.1007/s10530-013-0409-z

Griffin, A. S. (2016). Innovativeness as an emergent property: A new alignment of comparative and experimental research on animal innovation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150544. https://doi.org/10.1098/rstb.2015.0544

Heger, T., & Jeschke, J. M. (2014). The enemy release hypothesis as a hierarchy of hypotheses. *Oikos*, *123*, 741–750. https://doi.org/10.1111/j.1600-0706.2013.01263.x

Heger, T., & Jeschke, J. M. (2018). Enemy release hypothesis. In J. M. Jeschke & T. Heger (Eds.), *Invasion biology: Hypotheses and evidence* (pp. 92–102). Wallingford, UK: CABI.

Holway, D. A., & Suarez, A. V. (1999). Animal behavior: An essential component of invasion biology. *Trends in Ecology & Evolution*, *14*, 328–330. https://doi.org/10.1016/S0169-5347(99)01636-5

Jaworski, C. C., Bompard, A., Genies, L., Amiens-Desneux, E., & Desneux, N. (2013). Preference and prey switching in a generalist predator attacking local and invasive alien pests. *PLoS One*, *8*, e82231. https://doi.org/10.1371/journal.pone.0082231

Jeschke, J. M., Keesing, F., & Ostfeld, R. S. (2013). Novel organisms: Comparing invasive species, GMOs, and emerging pathogens. *Ambio*, *42*, 541–548. https://doi.org/10.1007/s13280-013-0387-5

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, *17*, 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kelehear, C., & Shine, R. (2020). Tradeoffs between dispersal and reproduction at an invasion front of cane toads in tropical Australia. *Scientific Reports*, *10*, 1–7. https://doi.org/10.1038/s41598-019-57391-x

Langkilde, T. (2009). Invasive fire ants alter behavior and morphology of native lizards. *Ecology*, *90*, 208–217. https://doi.org/10.1890/08-0355.1

Lemon, J. (2006). Plotrix: A package in the red light district of R. *R-News*, *6*(4), 8–12.

Levitis, D. A., Lidicker, W. Z., & Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, *78*, 103–110. https://doi.org/10.1016/j.anbehav.2009.03.018

Liebl, A. L., & Martin, L. B. (2014). Living on the edge: Range edge birds consume novel foods sooner than established ones. *Behavioral Ecology*, *25*, 1089–1096. https://doi.org/10.1093/beheco/aru089

Llewelyn, J., Webb, J. K., Schwarzkopf, L., Alford, R., & Shine, R. (2010). Behavioural responses of carnivorous marsupials (*Planigale maculata*) to toxic invasive cane toads (*Bufo marinus*). *Austral Ecology*, *35*, 560–567. https://doi.org/10.1111/j.1442-9993.2009.02067.x

Mandrillon, A. L., & Saglio, P. (2007). Herbicide exposure affects the chemical recognition of a non native predator in common toad tadpoles (*Bufo bufo*). *Chemoecology*, *17*, 31–36. https://doi.org/10.1007/s00049-006-0354-8

McFarland, K., Donaghy, L., & Volety, A. K. (2013). Effect of acute salinity changes on hemolymph osmolality and clearance rate of the non-native mussel, *Perna viridis*, and the native oyster, *Crassostrea virginica*, in Southwest Florida. *Aquatic Invasions*, *8*, 299–310. https://doi.org/10.3391/ai.2013.8.3.06

Mennen, G. J., & Laskowski, K. L. (2018). Defence is the best offence: Invasive prey behaviour is more important than native predator behaviour. *Animal Behaviour*, *138*, 157–164. https://doi.org/10.1016/j.anbehav.2018.02.017

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *Journal of Clinical Epidemiology*, *62*, 1006–1012. https://doi.org/10.1016/j.jclinepi.2009.06.005

Moseby, K. E., Cameron, A., & Crisp, H. A. (2012). Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? *Animal Behaviour*, *83*, 1011–1021. https://doi.org/10.1016/j.anbehav.2012.01.023

Overington, S. E., Morand-Ferron, J., Boogert, N. J., & Lefebvre, L. (2009). Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour*, *78*, 1001–1010. https://doi.org/10.1016/j.anbehav.2009.06.033

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Robert, M., & Sorci, G. (1999). Rapid increase of host defence against brood parasites in a recently parasitized area: The case of village weavers in Hispaniola. *Proceedings of the Royal Society B: Biological Sciences*, *266*, 941–946. https://doi.org/10.1098/rspb.1999.0727

Robertson, B. A., Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology & Evolution*, *28*, 552–560. https://doi.org/10.1016/j.tree.2013.04.004

Rosenthal, M. F., Gertler, M., Hamilton, A. D., Prasad, S., & Andrade, M. C. B. (2017). Taxonomic bias in animal behaviour publications. *Animal Behaviour*, *127*, 83–89. https://doi.org/10.1016/j.anbehav.2017.02.017

Ruland, F., & Jeschke, J. M. (2020). Data from: How biological invasions affect animal behaviour: A global cross-taxonomic analysis. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.573n5tb56

Saul, W.-C., & Jeschke, J. M. (2015). Eco-evolutionary experience in novel species interactions. *Ecology Letters*, *18*, 236–245. https://doi.org/10.1111/ele.12408

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*, 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Sih, A., Trimmer, P. C., & Ehlman, S. M. (2016). A conceptual framework for understanding behavioral responses to HIREC. *Current Opinion in Behavioral Sciences*, *12*, 109–114. https://doi.org/10.1016/j.cobeha.2016.09.014

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 5460–5465. https://doi.org/10.1073/pnas.0408145102

Sol, D., & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, *90*, 599–605. https://doi.org/10.1034/j.1600-0706.2000.900317.x

Stellatelli, O. A., Vega, L. E., Block, C., & Cruz, F. B. (2013). Effects on the thermoregulatory efficiency by two native lizards as a consequence of the habitat modification by the introduction of the exotic tree *Acacia longifolia*. *Journal of Thermal Biology*, *38*, 135–142. https://doi.org/10.1016/j.jtherbio.2012.12.005

Strauss, S. Y., Lau, J. A., & Carroll, S. P. (2006). Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? *Ecology Letters*, *9*, 357–374. https://doi.org/10.1111/j.1461-0248.2005.00874.x

Strayer, D. L., D'Antonio, C. M., Essl, F., Fowler, M. S., Geist, J., Hilt, S., … Jeschke, J. M. (2017). Boom-bust dynamics in biological invasions: Towards an improved application of the concept. *Ecology Letters*, *20*, 1337–1350. https://doi.org/10.1111/ele.12822

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, *21*, 645–651. https://doi.org/10.1016/j.tree.2006.07.007

Tinghitella, R. M., & Zuk, M. (2009). Asymmetric mating preferences accommodated the rapid evolutionary loss of a sexual signal. *Evolution*, *63*, 2087–2098. https://doi.org/10.1111/j.1558-5646.2009.00698.x

Torchiano, M. (2020). *effsize: Efficient effect size computation*. https://doi.org/10.5281/zenodo.1480624

Trewavas, A. (2014). *Plant behaviour and intelligence*. Oxford, UK: Oxford University Press.

Vanderwerf, E. A. (2012). Evolution of nesting height in an endangered Hawaiian forest bird in response to a non-native predator. *Conservation Biology*, *26*, 905–911. https://doi.org/10.1111/j.1523-1739.2012.01877.x

Vilà, M., & Hulme, P. E. (Eds.). (2017). *Impact of biological invasions on ecosystem services*. Cham, Switzerland: Springer.

Wagner, A. (2017). The white-knight hypothesis, or does the environment limit innovations? *Trends in Ecology & Evolution*, *32*, 131–140. https://doi.org/10.1016/j.tree.2016.10.017

Weis, J. S., & Sol, D. (Eds.). (2016). *Biological invasions and animal behaviour*. Cambridge, UK: Cambridge University Press.

Willer, C. J., Li, Y., & Abecasis, G. R. (2010). METAL: Fast and efficient meta-analysis of genomewide association scans. *Bioinformatics*, *26*, 2190–2191. https://doi.org/10.1093/bioinformatics/btq340

Wlodarczyk, R., & Janiszewski, T. (2014). Can expansion of zebra mussel, *Dreissena polymorpha* (Bivalvia) influence the numbers and behaviour of traditionally herbivorous mute swan, *Cygnus olor* (Aves)? *Acta Zoologica Bulgarica*, *66*, 235–238.

Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*, 665–673. https://doi.org/10.1093/beheco/aru183

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010). Behavioral flexibility and species invasions: The adaptive flexibility hypothesis. *Ethology Ecology & Evolution*, *22*, 393–404. https://doi.org/10.1080/03949370.2010.505580

York, C. A., & Bartol, I. K. (2016). Anti-predator behavior of squid throughout ontogeny. *Journal of Experimental Marine Biology and Ecology*, *480*, 26–35. https://doi.org/10.1016/j.jembe.2016.03.011

Zaykin, D. V. (2011). Optimally weighted Z-test is a powerful method for combining probabilities in meta-analysis. *Journal of Evolutionary Biology*, *24*, 1836–1841. https://doi.org/10.1111/j.1420-9101.2011.02297.x

Zuk, M., Bastiaans, E., Langkilde, T., & Swanger, E. (2014). The role of behaviour in the establishment of novel traits. *Animal Behaviour*, *92*, 333–344. https://doi.org/10.1016/j.anbehav.2014.02.032

SUPPORTING INFORMATION

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