A famous failure: Why were cane toads an ineffective biocontrol in Australia?

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Abstract
In 1935, cane toads (Rhinella marina) were brought to Australia to control insect pests. The devastating ecological impacts of that introduction have attracted extensive research, but the toads' impact on their original targets has never been evaluated. Our analyses confirm that sugar production did not increase significantly after the anurans were released, possibly because toads reduced rates of predation on beetle pests by consuming some of the native predators of those beetles (ants), fatally poisoning others (varanid lizards), and increasing abundances of crop-eating rodents (that can consume toads without ill-effect). In short, any direct benefit of toads on agricultural production (via consumption of insect pests) likely was outweighed by negative effects that were mediated via the toads' impacts on other taxa. Like the toad's impacts on native wildlife, indirect ecological effects of the invader may have outweighed direct effects of toads on crop production.

Keywords
agriculture, Anura, biocontrol, Bufo marinus, invasive species, mesopredator release, predation

1 | INTRODUCTION

As in many branches of science, detailed research on “model systems” has advanced our understanding of biological invasions (Kueffer, Pyšek, & Richardson, 2013). Even in intensively-studied systems, however, gaps in knowledge remain. For example, we often have extensive information about an invasive species within its new range but not within its native distribution (Shine, 2010); or we understand current impacts but lack background information about the history of range expansion (Vermeij, 1996). In this paper, we address a major knowledge gap in an intensively-studied invasion: the introduction and spread of the cane toad (Rhinella marina) in Australia.

The cane toad’s devastating ecological impact on Australian wildlife (Shine, 2010) has stimulated extensive research on the history of the toad’s translocation to Australia (e.g., Turvey, 2013), on the rates and routes of the toads’ range expansion within that continent (Urban, Phillips, Skelly, & Shine, 2008) and on the evolutionary and ecological consequences of the toad invasion (Brown, Phillips, & Shine, 2011; Brown, Ujvari, Madsen, & Shine, 2013; Phillips, Brown, & Shine, 2010). The rationale for the toad’s introduction to Australia in 1935 is clear: agricultural scientists at the Bureau of Sugar Experiment Stations brought 101 toads from Hawai‘i, bred them, and released their progeny along the Queensland coast to consume scarab beetles whose root-feeding larvae were major pests of commercial agriculture (Turvey, 2013). In particular, it was hoped that the toads would reduce abundances of two major pests, the French Beetle (Lepidiota [Batocera] frenchi) and the Greyback...
Beetle (*Dermolepida albohirtum*), and several other minor pests (*Lepidiota squamulata, L. caudata, L. crinita*, and others).

This attempt at biocontrol has been universally condemned as a failure and lampooned as a scientific blunder (e.g., Lever, 2001; Turvey, 2013). However, hard evidence is lacking. The conclusion that toads did not improve crop yields is based on general statements (not quantitative analyses) made by the people who brought the toad to Australia (Turvey, 2013). The idea that a generalist anuran predator might eat enough pest insects to improve crop yields is not implausible; the use of toads to control pests had a long history of success not only in domestic gardens (Turvey, 2013), but also (supposedly) in commercial sugar-cane plantations (Mungomery, 1935; Van Volkenberg, 1935; Wolcott, 1937). Indeed, Tucker and Wolcott (1936) claimed that the introduction of cane toads to sugar-cane plantations in Puerto Rico offers “one of the few instances on record of a foreign predator being entirely successful in the control of a native insect pest”.

The idea also gains support from recent field experiments: by introducing Chinese bullfrogs (*Hoplobatrachus rugulosus*), Teng et al. (2016) reduced populations of rice leaf rollers, stem borers, and plant hoppers, thereby increasing rice production in paddy-fields by >40% (see also Khatiwada et al., 2016). So, did cane toads really fail to control insect pests in Australia? And if so, why?

## 2 | IMPACT OF CANE TOADS ON AGRICULTURAL PRODUCTION

The toads brought to Australia in 1935 were bred, and hundreds of thousands of their offspring were released in sugar plantations of coastal Queensland over the next year (Turvey, 2013). Lacking data on exact locations and timing of releases, we cannot analyse toad impacts with a BACI design; instead, we can simply examine whether overall crop yields changed over time. We used intervention analysis to ask whether yields of sugar cane in Queensland plantations changed in 1935 (based on data in a review by the Queensland Bureau of Sugar Experiment Stations, 1950, the group that introduced the cane toad to Australia). This technique divides a time series into periods before, during and after some intervention event (such as the introduction of cane toads). It calculates a trend line for the dependent variable through time prior to the intervention, and asks whether the slope or elevation of that line shifts and changes slope at the critical time period. The method overcomes statistical problems associated with autocorrelation among variables (such as sugar yield) through successive time periods, thereby allowing a time-series approach using an autoregressive integrated moving average (see Brown et al., 2011 for a detailed explanation of this method).

Yields of sugar cane per hectare exhibited an overall increase over time between 1900 and 1949 (*F*\(_{1,46} = 6.52, p = .014; 95\% \text{ CIs for year effect} = 0.02–0.21\)). However, yields did not step upward concurrent with the introduction of toads in 1935 (*F*\(_{1,46} = .58; 95\% \text{ CIs} = −2.35–4.19\)) nor increase annually over background levels subsequent to toad introduction (*F*\(_{1,46} = .47; 95\% \text{ CIs} = −0.40–0.27\)) contrary to the scientists’ hope that introduction of cane toads would enhance productivity (Figure 1). These data support the agricultural scientists’ subjective assessment (see above): the introduction of cane toads failed to enhance crop yields. To explore why this happened, we can examine potential mechanisms by which the arrival of toads may have affected crop yields (below).

## 3 | MECHANISMS OF IMPACT OF CANE TOADS

### 3.1 | Consumption of insect pests

Cane toads have generalized diets, but with a consistent focus on ants and beetles (e.g., Dexter, 1932). The beetle species important in reducing sugar yield were very abundant in plantations, and the introduced cane toads doubtless consumed many of those pests (e.g., analysis of stomach contents of cane toads in Puerto Rico and Australia reported that most of the insects consumed were species adjudged to be harmful to the commercial crop: Dexter, 1932; Turvey, 2013). However, we cannot assess the impact of the toads’ beetle consumption on crop yields without data on toad abundances, feeding rates and diets, and on the relationship between beetle abundance and beetle-induced crop damage. We have none of those data.

### 3.2 | Consumption of nontarget insects

As well as consuming the pests they were intended to target, the broad diets of the introduced anurans meant that they ate many other invertebrates—at least some of which consumed beetles. Potentially, any beneficial effect of toads on beetle abundance may have been reversed by the introduced anuran’s predation on species that had previously helped to keep beetle numbers in check. Although we cannot quantify the intensity of impact, we know that cane toads eat vast numbers of ants across a wide range of habitat types (e.g., Evans & Lampo, 1996; Freeland, Delvinquier, & Bonnin, 1986; Heise-Pavlov & Longway, 2011; Isaacs & Hoyos, 2010; Mungomery, 1936;
including sugar-cane plantations (Dexter, 1932) and that ants can be effective predators of beetles and their larvae (e.g., López & Potter, 2000; Way & Khoo, 1992). Hence, consumption of “beneficial” insects by cane toads may have increased rates of consumption of sugar cane by beetles (as in the example of toad impacts in rice paddies: Shuman-Goodier et al., 2019).

### 3.3 Fatal poisoning of apex predators

The arrival of cane toads kills frog-eating predators that cannot tolerate the toad’s toxins (Shine, 2010). Most importantly, toad invasion decimates populations of previously-abundant varanid lizards (“goannas”), causing a dramatic decline in rates of predation on smaller species—and thus, increases in the abundance of those former prey (e.g., Doody et al., 2006; Doody et al., 2015; Jolly, Shine, & Greenlees, 2015). Toad-induced mortality of beetle-eating lizards could reverse any beneficial effect of beetle-eating toads.

Varanid lizards frequently consume both larval and adult beetles (e.g., Jessop, Urus, Lockwood, & Gillespie, 2010; Losos & Greene, 1988). *Varanus panoptes* is a large varanid that is distributed from coastal Queensland to coastal Western Australia and is severely affected by the arrival of cane toads (Ward-Fear, Pearson, Brown, Balanggarra Rangers, & Shine, 2016). Analyses of varanid scats from a floodplain habitat in northwestern Australia showed that for 2 months at the beginning of their activity season each year (Nov–Dec), these large lizards fed almost exclusively on recently metamorphosed cane beetles (*Lepidiota squamulata*), a declared pest of sugar cane plantations at the time of cane toad introduction, and a congener of the beetle species that cane toads were primarily introduced to control (Ward-Fear, Brown, & Shine, 2020). We found cane beetles in 47 of 52 scats (90%) collected over this period, with an average of 13.2 beetle heads per scat (range 0–40, SE = 1.98). The lizards’ rate of beetle consumption fell later in the year, after adult beetles had completed their 1-year lifecycle (with native rodents becoming the major prey: Ward-Fear et al., 2020). This early-season predation on emerging beetles would reduce the abundance of these pests across their mating period (Settle et al., 1996).

### 3.4 Benefits for other agricultural pests

Native rats are a major pest in sugar-cane plantations, reducing crop yields by up to 30% (Dyer, 2010; Hood, Nass, Lindsey, & Hirata, 1971; Samson, Sallam, & Chandler, 2013). Most Australian rodents are not affected by cane toad toxins, and readily eat these anurans (Cabrera-Guzmán, Crossland, Pearson, Webb, & Shine, 2015). Any increase in
rat abundance due to this additional prey resource would have been amplified by the reduced rate of predation on rodents by varanid lizards (poisoned by toads—see above). In the above study of *V. panoptes*, the remains of rodents were found in 12 of 22 varanid scats (45%) collected during the dry-season (May–July: Ward-Fear et al., 2020), the peak period of juvenile recruitment and the onset of serious damage to sugar crops (Dyer, 2010).

4 | DISCUSSION

Our analyses support the idea that cane toads failed to control insect pests, and suggest reasons for that failure. Although toads consumed many beetles, they also would have killed native predators of those pests by eating them and by fatally poisoning them. Toad introduction may also have benefitted rodent populations by providing additional food and reducing the risk of predation. Increasing the abundance of crop-consuming beetles and rats (during their peak reproductive phases) would tend to negate any crop-yield benefits accruing from consumption of beetles by toads. Under this scenario, the indirect effects of cane toads on sugar yield were eclipsed by indirect effects, mediated via the toad’s impact on native predators. The same conclusion has been reached from studies on the ecological impact of cane toads on Australian wildlife (e.g., Doody et al., 2006, 2015; Jolly et al., 2015; Shine, 2010).

The relative importance of direct and indirect effects will differ among systems, as a function of local habitat characteristics, climate, and biotic assemblages. Nonetheless, some patterns may be widespread. For example, a recent study from the Philippines suggested that ants are beneficial to the rice crop (as predators of pest species), and that heavy predation on ants by introduced cane toads may allow populations of pest insects to increase (Shuman-Goodyer et al., 2019). The same mechanism may apply in Australian sugar-cane plantations. Plausibly, a significant number of the larger invertebrates and small vertebrates eaten by cane toads also may have consumed beetles that would otherwise have attacked sugar cane.

The scientists who brought cane toads to Australia gave little thought to possible impacts on native wildlife (Turvey, 2013), and (as far as we know) did not consider the possibility of indirect facilitation of beetle populations via toad-induced mortality of native predators. It is easy to be critical in hindsight, and one strong implication of our analysis is the difficulty of predicting impacts of a bio-control agent in advance. Direct impacts can be assessed (e.g., will the novel agent kill or compete with native organisms?) but indirect impacts, mediated by trophic links, will be harder to predict. In many cases, the existence of such links become apparent only after they are disrupted by an invader (as has occurred with varanid lizards, where the toad invasion has shown us that varanids are critically important for ecosystem function in tropical Australia: Brown et al., 2013; Doody et al., 2015).

In summary, our analysis provides empirical support for an assertion that was previously speculative; suggests a commonality between invader impacts on agricultural production versus on native ecosystems; and reinforces the difficulty of predicting invader impacts a priori.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

Richard Shine devised the project, Gregory P. Brown conducted statistical analyses, all three authors contributed to writing the manuscript.

DATA AVAILABILITY STATEMENT

Data are available at Dryad doi:10.5061/dryad.v9s4mw6t8

ETHICS STATEMENT

This research was approved by the University of Sydney’s Animal Ethics Committee (Protocol: 2103/6034, DBCA permit: SF010079), in accordance with the international “Principles of Laboratory Animal Care” as well as the “Australian Code for the Care and Use of Animals for Scientific Purposes.”

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