RESEARCH ARTICLE

Cost-benefit evaluation of management strategies for an invasive amphibian with a stage-structured model

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Abstract

Management strategies for invasive populations should be designed to maximise efficacy and efficiency, i.e. to accomplish their goals while operating with the least resource consumption. This optimisation is often difficult to achieve in stage-structured populations, because costs, benefits and feasibility of removing individuals may vary with stage. We use a spatially-explicit stage-structured model to assess efficacy of past, present and alternative control strategies for invasive guttural toads, *Sclerophrys gutturalis*, in Cape Town. The strategies involve removal of variable proportions of individuals at different life-history stages and spatial scales. We also quantify the time necessary to implement each strategy as a proxy of financial resources and we correct strategy outcomes by implementation of time to estimate efficiency. We found that the strategy initially pursued in Cape Town, which did not target any specific stage, was less efficient than the present strategy, which prioritises adult removal. The initial strategy was particularly inefficient because it did not reduce the population size despite allocating consistent resources to remove eggs and tadpoles. We also found that such removal might be detrimental when applied at high levels. This counter-intuitive outcome is due to the 'hydra effect': an undesired increase in population size caused by removing individuals before overcompensatory density dependence. Strategies that exclusively remove adults ensure much greater management efficiency than those that also remove eggs and tadpoles. Available management resources should rather be allocated to increase the proportion of adult guttural toads that are removed or the spatial extent at which this removal is pursued.

Keywords

Density dependence, hydra effect, invasive species, management costs, overcompensation, spatially-explicit model

Introduction

Management strategies for invasive populations often aim to eradicate or control the number of invasive individuals in order to minimise their impacts on native species, ecosystems and human activities (Bomford and O'Brien 1995; Robertson et al. 2020). Ideally, these strategies should be designed to maximise both efficacy and efficiency, i.e. to fully accomplish their intended goals while functioning with the least expenditure of resources (Blackwood et al. 2010; Epanchin-Niell and Hastings 2010; Bonneau et al. 2017; Nishimoto et al. 2021). When designing strategies for invasive populations, it is, therefore, desirable to predict not only their absolute outcomes, but also outcomes per unit of resources used (Epanchin-Niell and Hastings 2010; Januchowski-Hartley et al. 2011; Epanchin-Niell and Wilen 2012).

Numerous invasive populations are characterised, at any given time, by cohorts of different life-history stages (also called stage-structured populations; Rodrigues et al. 2015; Hui and Richardson 2017). To maximise reductions in rates of population growth or range expansion, these populations can be eradicated or controlled by allocating a disproportionate management effort towards one or a few specific life-history stages (Ramula et al. 2008; Pichancourt and van Klinken 2012). Deciding on which stage must be prioritised for removal is, however, not always straightforward, because costs and feasibility of removing individuals can vary significantly with their stage in both plants (Taylor and Hastings 2004; Blackwood et al. 2010; Pichancourt and van Klinken 2012) and animals (Buhle et al. 2005; Day et al. 2018). For instance, adult stages are often characterised by fewer individuals, but higher survival rates, than juvenile stages (Lampo and De Leo 1998; Buckley et al. 2005; Govindarajulu et al. 2005; Pardini et al. 2009). Adult and juvenile stages may also be characterised by contrasting behavioural and dispersal capabilities (Govindarajulu et al. 2005; Jongejans et al. 2008; Vimercati et al. 2021) or size and physiology (Beaty and Salice 2013; Green et al. 2014).

Stage-related differences may affect not only the number of individuals that can be detected (detection probability) or removed after detection (intervention success rate), but also how many individuals from different stages can be removed per unit of resource invested (Taylor and Hastings 2004; Mehta et al. 2007; Epanchin-Niell and Hastings 2010). It follows that strategies designed to eradicate or control alien populations often target stages whose individuals are the easiest to detect or remove. This opportunistic approach, however, does not necessarily translate into significant reductions in population size, especially when complex population dynamics exist. For instance, strategies based on the use of electrofishing to control the invasive smallmouth bass, *Micropterus dolomieu*, removed mainly adults, a condition that led to enhance both juvenile recruitment and survival and, consequently, to increase population size (i.e. overcompensation; Weidel et al. 2007; Loppnow and Venturelli 2014). Similarly, applications of herbicides at the rosette stage of the invasive garlic mustard, *Alliaria petiolata*, were largely inefficient in reducing adult abundance, because the initial demographic effects on the rosette density were entirely counterbalanced by marked density dependence survival later in the life-cycle (Pardini et al. 2009). Whenever possible, invasive species

population dynamics and information regarding management expenditure should thus be combined to design strategies that maximise outcome while minimising costs.

Invasion dynamics can be reconstructed using a range of mathematical models operating at both individual and population level in accordance with predefined ecological and evolutionary rules (Hastings et al. 2005; Jongejans et al. 2008; Schreiber and Lloyd-Smith 2009; Hui and Richardson 2017). When these models are built to simulate alternative strategies, based on removal of various proportions of individuals at different stages (Buckley et al. 2005; Pardini et al. 2009; Loppnow and Venturelli 2014), strategy outcomes can be corrected by implementation costs to estimate management efficiency (Taylor and Hastings 2004; Epanchin-Niell and Hastings 2010; Epanchin-Niell and Wilen 2012).

In this paper, we assess efficacy and efficiency of alternative management strategies for an invasive population of the guttural toad, *Sclerophrys gutturalis* (Power, 1927), in a peri-urban residential area of Cape Town (Measey et al. 2017). Invasive guttural toads, which were first detected in Cape Town in 2000 (de Villiers 2006), use garden ponds for breeding (Vimercati et al. 2017a, b) and have adaptively responded to the unfamiliar environmental settings of the invasive range (Vimercati et al. 2018, 2019; Madelaire et al. 2020; Barsotti et al. 2021; Mühlenhaupt et al. 2021). In 2010, the City of Cape Town contracted a private company to decrease the population size and limit expansion of the invasive population (Davies et al. 2020a, b) by removing toads from their breeding sites. The breeding sites were mostly located in private properties to which access must be granted by the owners (Vimercati et al. 2017b). In the initial phase of the control operation (2011–2016), adults were disproportionately targeted for removal, although juveniles, metamorphs, tadpoles and eggs were also opportunistically removed (Vimercati et al. 2017a). This strategy was altered in 2017, when data from a preliminary simulation study showed that the removal of eggs and tadpoles reduced the invasive population size to a lesser extent than the removal of adults (Vimercati 2017; Davies et al. 2020b). Consequently, control personnel stopped targeting pre-metamorphic individuals and allocated all management efforts to adult and juvenile removal, a strategy that is currently being pursued (Davies et al. 2020b).

In this study, we explain the rationale behind the decision to change strategies in the control operation of the guttural toad in Cape Town. For management strategies involving the removal of variable proportions of individuals at different life-history stages, efficacy and efficiency were assessed here by the use of a spatially-explicit stage-structured model, which has already been parameterised and validated for this invasive population with field data (Vimercati et al. 2017b). The model has already been used in a recent simulation study to test the efficacy of multiple management strategies based on the removal of a fixed proportion of adult toads at different spatial scales (Vimercati et al. 2017a). This simulation study found that the removal of adults from sites accessible for management did not markedly alter the invasive population size (Vimercati et al. 2017a), because the control team was only able to access a minority of the residential properties located in the area. Hence, we ask here whether a further removal of individuals at other stages, such as juveniles, tadpoles and eggs, may im-

prove management efficacy. As a proxy for financial costs, we also quantify the time necessary to implement alternative management strategies in order to estimate their net efficiency, i.e. their outcome per unit of resource used.

Methods

Model structure

The stage-structured model proposed by Vimercati et al. (2017b) uses a set of integrodifference equations to simulate the spatial dynamics of the invasive guttural toad population in Cape Town within a network of 415 ponds over an area of 27 km^2. The location and size (i.e. small, medium or large) of each pond were obtained through aerial imaging and validated through ground-truthing. In the model, the pond network acts as a meta-population where each pond exchanges individuals with other ponds as a function of a species' dispersal kernel and landscape resistance costs. Within each pond, demographic dynamics are simulated across five life-history stages (i.e. adults, juveniles, metamorphs, tadpoles and eggs). Within the pond network, dispersal dynamics are simulated across two life-history stages (i.e. adults and juveniles). The model realistically captures the life-cycle and invasion dynamics of the guttural toad in Cape Town. Density-independent traits (e.g. adult survival rate and clutch size), density-dependent traits (e.g. tadpole survival rate), detailed integrodifference equations and descriptions of the model are presented in Vimercati et al. (2017b) and summarised in Suppl. material 1.

In brief, an average of 13000 eggs are laid twice a year by each female from late spring (October-November) to late summer (February), with the probability for females to lay eggs in a pond that varies with pond size (Vimercati et al. 2017b). Tadpoles hatch from eggs in one week assuming a constant survival rate (0.7 per individual) and methamorphose in 4–5 weeks as a function of their density in the pond. Over-wintering metamorphs emerge the next spring as juveniles with a probability that varies with their density at the pond edge. Juveniles survive and mature into adults in one year assuming constant rates (0.2 and 0.25 per individual), while adults also survive at a constant rate (0.6 per individual). Each year, fixed proportions of juveniles (0.34) and adults (0.2) disperse across the pond network.

As the population size is reasonably large, demographic stochasticity can be safely ignored; the peri-urban environment has further reduced any effects from environmental fluctuation and uncertainty. First, invasive guttural toads in Cape Town use only permanent, mainly artificial, ponds, thus justifying the assumption that the pond network does not change over time. Second, given the small spatial scale of the invaded area, the climate can be considered homogeneous across the whole pond network, while the landscape structure has not been altered since the first introduction of the species in Cape Town (Vimercati et al. 2017b). Consequently, all life-history traits are set to constant values and landscape features and resistance costs are modelled deterministically. In addition, the model results are robust to changes in the values of most

life-history traits, except for changes in the juvenile and adult survival rates which were estimated according to studies on similar species (Vimercati et al. 2017b). The model proceeds for 30 time-steps to simulate 30 years of annual population dynamics, from 2001 (i.e. when the species was first recorded in a single pond of Cape Town) to 2030.

Management simulation

The model structure allows the alteration of mortality rate of any stage at any point in space (different ponds) and time (different years). As a consequence, this model can be used to test alternative management strategies based on different rates of removal across stages (Vimercati et al. 2017a). In accordance with the study conducted by Vimercati et al. (2017a), management strategies were simulated to start in 2011 (i.e. the actual starting year of the management actions in Cape Town) and to end in late 2020. This interval had been chosen to explore the degree to which the alien population can recover in a ten-year period (2021–2030) after management.

First, we designed a management strategy named "initial removal", which realistically simulates removal of the guttural toad in Cape Town from accessible ponds as pursued from 2011 to 2016 by the implementation team (i.e. 128 ponds, see also Vimercati et al. 2017a). As this strategy was implemented in Cape Town without preferentially removing any specific stage (Davies et al. 2020a), we assume, for simplicity, that the proportion of individuals removed across different stages emerges from the interplay between implementers' removal capacity and spatial and temporal occurrence of each stage class in and around the pond. For instance, the proportion of tadpoles that can be removed is expected to be low (0.25), because tadpoles are difficult to detect and capture (e.g. by netting) and they stay in the pond for only 4–5 weeks before metamorphosing. Conversely, the proportion of adults removed from a pond should be high (0.8), because individuals, at this stage, are relatively easy to detect, given their large body size (females) and advertisement calls (males), and they also congregate in or around the pond during the breeding season. The proportions of individuals that are removed for each stage class, according to the "initial removal" strategy and their rationale, are reported in Table 1. Although these proportions may not be exact, field survey, field data and consultation with implementers showed they are realistic (see last column in Table 1 for detailed explanations).

Second, we test a management strategy named "adult removal", which simulates the exclusive removal of adults from ponds accessible to the implementation team. This strategy is currently being pursued in Cape Town, shares with the "initial removal" strategy the proportion of adults removed from each pond (0.8), but differs in that no other stages are targeted for removal. To test whether individuals at early life-history stages should be prioritised over adults, we additionally simulated a third "pre-metamorphic removal" strategy, which is based on the exclusive removal of the same proportion of eggs and tadpoles (0.8) from accessible ponds. We also simulated the hypothetical application of the above three strategies across all ponds (i.e. accessible and not-accessible ponds) in order to explore how management efficacy and efficiency

Table 1. Proportions of guttural toads, *Sclerophrys gutturalis*, removed in Cape Town from ponds accessible by implementers according to the "initial removal" strategy simulated with the stage-structured model. For each stage, the proportion of individuals removed has been estimated by considering: the removal capacity by the implementation team; the spatial and temporal occurrence of the stage in the property visited by the team. Removal proportions have been confirmed by using evidence collected from field data and surveys.

Stage	Proportion of individuals removed	Removal capacity by the implementation team	Spatial occurrence	Temporal occurrence	Evidence from field data and surveys
Adult	0.8	**High.** Most males and females can be easily detected by the implementation team in and around the pond because of the large body size (Snout to Vent Length [SVL], > 45 mm) and breeding behaviour (e.g. calling in males).	**High.** Most males and females congregate in and around the pond during the reproductive season.	**Medium.** Most males call and stay in and around the pond during the whole reproductive period. Females stay in and around the pond only until the end of egg laying.	Most of the post-metamorphic individuals captured during the management programme were adults (70%). The number of adults removed in a pond at first visit was on average significantly higher than the number of adults detected at second visit.
Juvenile	0.05	**Low.** Juveniles are difficult to detect because of the small body size (15 < SVL < 45 mm) and the absence of breeding behaviour.	**Low.** Juveniles do not congregate in or around the pond, but are more equally distributed across the invaded area.	**Low.** Juveniles do not congregate in or around the pond during the breeding season.	Only 30% of post-metamorphic individuals captured during the management programme were juveniles. However, the model built in Vimercati et al. (2017b) and other similar models on amphibians (e.g. Beaty and Salice 2013) forecast a number of juveniles between three and ten times higher than the number of adults in the same population. Such a discrepancy between the number of juveniles captured and those that are expected to be present in the population suggests that individuals at this stage are extremely difficult to find.
Metamorph	0.25	**Low.** Metamorphs are extremely difficult to detect by the implementation team because of the small size (SVL < 15 mm). Additionally, their high density around the pond makes the removal time-consuming.	**High.** Metamorphs stay around the pond edge (within a radius of 5 m) for some weeks after metamorphosis.	**Medium.** Metamorphs stay around the pond for some weeks only after metamorphosis.	Most metamorphs (90%) were detected only during the second part of the breeding season (middle December-February). When metamorphs were detected around a pond, the implementation team succeeded in removing only a minority of them around the pond.
Tadpole	0.25	**Low.** Tadpoles are extremely difficult to detect and remove by netting in the pond, especially during the night.	**High.** Tadpoles stay in the pond although their removal is more difficult in large ponds.	**Medium.** Tadpoles stay in the pond for 4–5 weeks before metamorphosis.	Tadpoles were removed across the entire breeding season. In most cases, the implementation team could not remove the majority of tadpoles in the pond.
Egg	0.05	**Low.** Eggs are extremely difficult to detect and remove by netting in the pond, especially during the night.	**High.** Eggs stay in the pond, although their removal is more difficult in large ponds.	**Low.** Eggs stay in the pond for only 5–7 days before hatching.	Eggs were detected and removed much less frequently than tadpoles during the management programme.

vary with restricted access. Analogous to Vimercati et al. (2017a), we additionally simulated a "no removal" strategy, in which the implementation team does not remove any individuals, and a "successful eradication" strategy, in which the removal of most adults, tadpoles and eggs from all ponds leads to a crash in the invasive population. Finally, we quantify to what extent increased efforts in removing eggs and tadpoles improve management efficacy by simulating strategies in which increasing proportions (from 0.6 to 1.0) of post-metamorphic individuals are removed from all ponds.

Efficacy and efficiency assessment

For each management strategy, we estimate efficacy (i.e. the degree to which a strategy accomplishes its goal) and net efficiency (i.e. the efficacy of a strategy corrected by the time [as a proxy for cost spent] on its implementation). As the goal of the initial management programme in Cape Town was to decrease the total number of invasive individuals to zero (i.e. full eradication, Davies et al. 2020b), we use the adult population size obtained just after the end of each simulated strategy (i.e. in 2021) as an inverse proxy for strategy efficacy. Consequently, strategies leading to smaller population sizes are considered more effective than those leading to larger population sizes. The adult population size obtained by simulating a "no removal" strategy (Table 2) is also set as a neutral baseline for efficacy, following Beaty and Salice (2013). As a result, the ratio of the difference between the baseline population size S_0 and the population size obtained by simulating a given strategy (hereafter called S_i) over the baseline population size represents the strategy efficacy E:

$$E = (S_0 - S_i) \tag{1}$$

In other words, E reflects how many invasive individuals would theoretically be removed from the population as a consequence of a given management strategy. For ease of comparison, we also calculate the efficacy in percentage (E%) from the ratio between E and S_0:

$$E\% = (S_0 - S_i) * 100 / S_0 \tag{2}$$

For each strategy, we measured efficiency F as the ratio between E and the strategy implementation cost T expressed in hours. Implementation costs can be estimated in various ways, for instance, by measuring average personnel salary or equipment cost. Here we assume that the management effort invested to control the guttural toad in Cape Town is linearly related to the time spent by the implementation team to remove the toads. This assumption is supported by the observation that the management of guttural toads is done manually without using expensive equipment, while the total salary costs of the implementation team reflect the time spent for removal. We thus conducted field surveys in 2014, 2015 and 2016 to estimate the time (in hours) spent by a manager to target each stage during the initial strategy of removal. We found that at each visit, 1, 0.25 and 0.5 hours have been, on average, allocated to remove adults and juveniles (T_{aj}), metamorphs (T_m) and tadpoles and eggs (T_{te}), respectively.

The removal of adults and juveniles was more time-consuming than the removal of metamorphs: while adults and juveniles can be detected only through a detailed walking survey of the area around the pond, metamorphs are generally found only within 1 to 5 metres from the pond edge, where they congregate to minimise desiccation risk (Vimercati et al. 2017a). The implementation team was also instructed to dedicate a significant portion of their time to detect adults in order to remove reproductive individuals (Scott Richardson, pers. comm.). We consider time spent to remove adults

Table 2. Proportions of guttural toads, *Sclerophrys gutturalis*, removed from each pond according to the different management strategies simulated with a stage-structured model. For each simulated strategy, number of ponds in which the removal is performed, rationale and total time necessary to perform the removal in one year (T) are reported. Please note that the "initial removal" strategy describes the ongoing management of the invasive population in Cape Town (see Table 1), whereas the other strategies describe alternative fictional strategies that could have been implemented.

Management strategy simulated through the stage-structured model described in Vimercati et al. (2017b)	Proportion of individuals removed from each stage in the simulated strategy					Number of ponds visited by the implementation team (N_p) / Total number of ponds in the area	Rationale behind the simulated strategy	Estimated total yearly time T (in hours) spent by the implementation team to remove individuals from different stages while visiting properties, as expressed in the formula (3): $(T_{aj} + T_m + T_{te}) \times 2 \times N_p = T$
	Ad.	Juv.	Met.	Tad.	Eggs			
"Initial removal"	0.8	0.05	0.25	0.25	0.05	128/415	Estimate of the initial management strategy in which the implementation team remove individuals at different stages from accessible ponds (See also Table 1)	$(1 + 0.25 + 0.5) \times 2 \times 128 = 448$
"Adult removal" (current strategy)	0.8	0	0	0	0	128/415	Fictional management strategy in which the implementation team removes only adults from accessible ponds	$(1 + 0 + 0) \times 2 \times 128 = 256$
"Pre-metamorphic removal"	0	0	0	0.8	0.8	128/415	Fictional management strategy in which the implementation team removes only eggs and tadpoles from accessible ponds	$(0 + 0 + 1.5) \times 2 \times 128 = 384$
"Initial removal in all ponds"	0.8	0.05	0.25	0.25	0.05	415/415	Estimated initial management strategy in which the implementation team removes individuals at different stages from all ponds	$(1 + 0.25 + 0.5) \times 2 \times 415 = 1453$
"Adult removal in all ponds"	0.8	0	0	0	0	415/415	Fictional management strategy in which the implementation team removes only adults from all ponds	$(1 + 0 + 0) \times 2 \times 415 = 830$
"Pre-metamorphic removal in all ponds"	0	0	0	0.8	0.8	415/415	Fictional management strategy in which the implementation team removes only eggs and tadpoles from all ponds	$(0 + 0 + 1.5) \times 2 \times 415 = 1245$
"No removal"	0	0	0	0	0	0/415	Fictional strategy in which the implementation team does not remove any individual	$(0 + 0 + 0) \times 0 \times 0 = 0$
"Successful eradication"	0.95	0	0	0.8	0.8	415/415	Fictional management strategy in which the implementation team removes most adults, eggs and tadpoles from all ponds	$(2 + 0 + 1.5) \times 2 \times 415 = 2905$

and juveniles as a single unit (T_{aj}), as our survey showed that the implementation team usually captures invasive individuals from both these stages within the same area and interval of time. An analogous assumption was made for tadpoles and eggs, which are simultaneously removed from the pond by sweep-netting. The total yearly time spent to remove individuals from different classes (T) is, therefore, obtained according to the following the formula:

$$T = (T_{aj} + T_m + T_{te}) \times N_p \times 2 \qquad (3)$$

where the time spent each night to remove individuals across different stages in a single property is multiplied by the number of properties that can be visited (N_p) in one year and by two, which is the average number of properties visited each night. The limited number of properties that can be visited each night by the team (i.e. two properties) is due to the necessity to remove toads when they are mostly active (i.e. within three-

four hours after sunset) and the obligation to gain access to a private property at a time that suits the owner (e.g. no later than midnight). As the guttural toad management programme employed only one team to remove toads in 2014, 2015 and 2016, all calculations are based on a single team visiting properties in the evening.

Results

The removal of most adult toads (80%) from accessible ponds ("adult removal" strategy) currently pursued in Cape Town is as effective as the initial strategy (Table 3, Fig. 1), in which adult removal was extended by an additional removal of juveniles, metamorphs, tadpoles and eggs (Table 3, Fig. 1, Suppl. material 2). Moreover, the "adult removal" strategy can be implemented at a lower cost (by 43% of hours spent for removal) than the initial strategy (Table 3, Suppl. material 2). Very similar results are obtained by simulating the application of the same two strategies across all ponds (Fig. 1), with the unique removal of adults that is almost twice as efficient as the initial mode of removal (Table 3, Suppl. material 2). Simultaneously removing individuals at early and late stages (e.g. adults and tadpoles) therefore seems inefficient, because such an intervention prolongs the time spent in each property by the implementation team without providing a commensurate decrease in the guttural toad population size. Intriguingly, our results also show that, when the removal of pre-metamorphic individuals is executed without removing adults in the same ponds ("pre-metamorphic removal" strategy), such a strategy increases the total number of adults in the population (Table 3, Suppl. material 2). Any additional increase in the proportion of eggs

Table 3. Population size at the end of management, efficacy, efficacy in percentage, cost T (in hours) and efficiency obtained by simulating different strategies with a stage-structured model for the invasive population of guttural toad, *Sclerophrys gutturalis*, in Cape Town. Note that the "initial removal" and "adult removal" strategies describe, respectively, the initial strategy (2011–2016, Table 1) and the ongoing strategy (2017-) implemented in Cape Town, whereas the other strategies describe alternative fictional strategies that could have been implemented. In bold, strategies that lead to counter-effective results, i.e. an increase in the population size at the end of management.

| Strategy	Population size at the end of management (2011)	Strategy efficacy E, as expressed in the formula (1)	Strategy efficacy E%, as expressed in the formula (2)	Strategy Implementation cost T expressed in hours (as reported in Table 1)	Strategy efficiency F expressed as the ratio between E and T
"No removal"	2973	–	0	0	–
"Initial removal"	2162	811	27%	448	1.81
"Adult removal"	2197	776	26%	256	3.03
"Pre-metamorphic removal"	**3318**	**- 345**	**Counter-effective**	**384**	**Counter-effective**
"Initial removal in all ponds"	494	2479	83%	1453	1.71
"Adult removal in all ponds"	465	2508	84%	830	3.02
"Pre-metamorphic removal in all ponds"	**3897**	**- 924**	**Counter-effective**	**1245**	**Counter-effective**
"Successful eradication"	0	2973	100%	2905	1.02
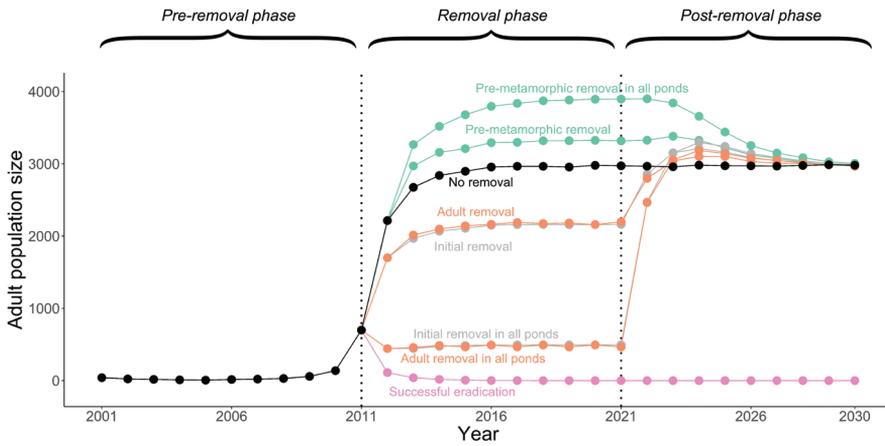
Figure 1. Population size of invasive toads estimated by a stage-structured model simulating alternative management strategies. Adult population size of invasive guttural toads, *Sclerophrys gutturalis*, in Cape Town estimated by a stage-structured model that simulates potential management strategies, as listed in Table 2. Colours (blue, red, grey and purple) indicate removal strategies that are hypothetically carried out by removing different age classes at contrasting spatial scales (accessible ponds vs. all ponds). Black indicates a no-removal scenario. Management was simulated to start in 2011 and to be interrupted in late 2020 (removal phase), after which the model simulating the invasive population would be allowed to run for a further 10 years until 2030. Estimated population size of each fictional management strategy is reported in Suppl. material 2.

and tadpoles removed from the ponds results in a further increase in the total population size (Fig. 2), whereas the full eradication of the population is achieved only by removing all eggs and tadpoles from all ponds. According to our model, the successful eradication of the invasive population could also be achieved by causing a population crash through the removal of almost all adults and most pre-metamorphic individuals from all ponds (Table 3, Fig. 1). The implementation cost of this management effort is estimated to be as much as six times more expensive than that of the initial management strategy (2905 hrs vs. 448 hrs, Table 3) and 11 times more expensive than the current strategy of adult removal (256 hrs).

Discussion

We found that the efficiency of the initial strategy adopted in Cape Town to control the guttural toad was impaired by the removal of eggs and tadpoles; their removal did not noticeably affect the population demography (Fig. 1), but rather subtracted resources (i.e. time) from other modes of removal (e.g. of adult toads). In other words, pre-metamorphic removal did not provide any significant demographic benefit (Table 3)
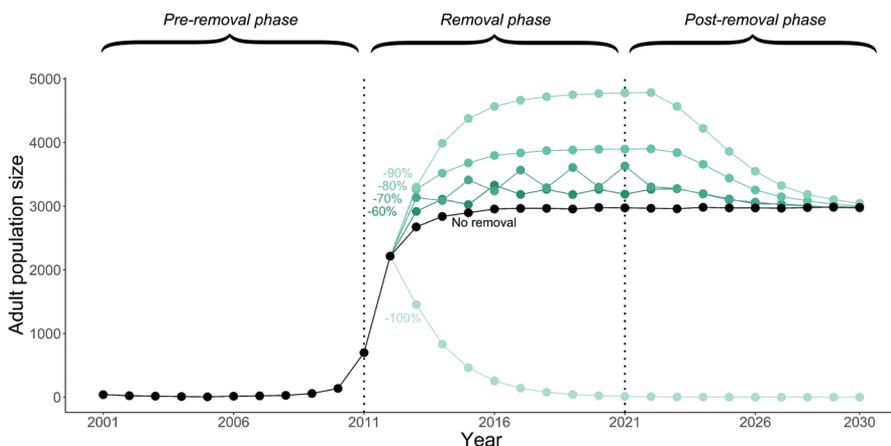
Figure 2. Population size of invasive toads estimated by a stage-structured model simulating different removal proportions of pre-metamorphic individuals. Adult population size of invasive guttural toads, *Sclerophrys gutturalis*, in Cape Town estimated by a stage-structured model that simulates different removal proportions of pre-metamorphic individuals (eggs and tadpoles). Colours indicate different proportions of removal expressed in percentage. Black indicates a no-removal scenario. Management was simulated to start in 2011 and to be interrupted in late 2020 (removal phase), after which the model simulating the invasive population would be allowed to run for a further 10 years until 2030.

and might have even been detrimental when applied with increasing intensity (Fig. 2). The partial removal of pre-metamorphic guttural toads as initially pursued was sub-optimal, while the strategy, currently implemented, ensures a much greater management efficiency (Table 1), albeit without leading to eradication (Davies et al. 2020b).

The counter-intuitive observation that a sustained removal of eggs and tadpoles may increase, rather than decrease, the adult population size can be explained by the occurrence of the 'hydra effect'; i.e. "the phenomenon of a population increasing in response to an increase in its per-capita mortality rate" (Abrams 2009). The hydra effect, also defined in some cases as overcompensation (Zipkin et al. 2009; Loopnow and Venturelli 2014; Schröder et al. 2014), has been detected in both structured and unstructured population models as well as in empirical studies (Govindarajulu et al. 2005; Zipkin et al. 2008; Hilker and Liz 2013; Schröder et al. 2014; McIntire and Juliano 2018). The hydra effect may be due to various mechanisms, such as altered patterns of demographic fluctuations (e.g. due to non-linear functional responses), reductions in resource exploitation rates from predators (e.g. due to prey switching from adaptive foraging) and temporal separation of mortality and density dependence (Abrams 2009). We advance that the last of these factors may explain why, in our model, simulated removals of eggs and tadpoles led to the occurrence of the hydra effect. In accordance with other stage-structured models on amphibians (Lampo and De Leo 1998; Vonesh and De la Cruz 2002; Govindarajulu et al. 2005), our model

explicitly incorporates density-dependent survival at the tadpole and metamorphic stages to simulate population regulatory processes occurring early in the life-cycle (Vimercati et al. 2017a). Such regulatory processes are common in larval and juvenile stages of anuran species, at least under experimental conditions (Wilbur 1977; Patrick et al. 2008; Berven 2009). However, in Cape Town, the removal of eggs performed by the implementation team increases mortality before the animals could reach the tadpole stage. Furthermore, the removal of tadpoles has been simulated as being performed only shortly after the tadpoles hatch from the eggs, i.e. before their survival is regulated by density dependence. As a consequence, the induced mortality caused by the implementation team "precedes and is concentrated in the early part of a strongly density-dependent stage", a condition that has been considered essential for the existence of the hydra effect (Abrams 2009; McIntire and Juliano 2018). A positive effect of mortality preceding density dependence seems quite common in structured populations (Abrams 2009; Pardini et al. 2009; Loppnow and Venturelli 2014; Schröder et al. 2014; McIntire and Juliano 2018) and should be routinely considered in management planning (Zipkin et al. 2009; Turner et al. 2016), for instance, implementing removal only after density-dependent phenomena (but see Hilker and Liz 2013). The existence of overcompensatory density dependence might also explain why, in native amphibians, low or variable survival rates at early life stages (eggs and tadpoles) have only a minor effect on population growth or decline, in comparison with low post-metamorphic survival rates (Vonesh and De la Cruz 2002; Petrovan and Schmidt 2019; Rose et al. 2021).

Since density dependence in tadpoles is also followed by density dependence in metamorphs, our study also shows that this condition promotes a relaxation of the density-dependent bottleneck; as a consequence, a higher equilibrium density is reached (Schröder et al. 2014). Intriguingly, this could also explain why, once the equilibrium population size is reached, we found a significant difference in adult density amongst ponds of a different size (see Suppl. material 2); small ponds were counterintuitively characterised by a higher number of adults than medium and large ponds. A further indication that higher equilibrium population sizes can be reached under the effect of sequential density-dependent processes comes from the number of individuals observed in the ponds at different life stages forecast by our model. During the saturation phase, small ponds are characterised by low numbers of eggs, tadpoles and metamorphs. However, the situation is completely reversed in juveniles, suggesting that metamorphic density-dependent survival occurring at the pond edge has a much more severe regulatory effect in large and medium ponds. This pattern is not observed in the first years of removal, i.e. when the population was not at the equilibrium, therefore limiting the possibility to implement a management strategy during the initial spread that maximises adult removal by targeting ponds with a specific size.

The occurrence of a strong positive mortality effect at the population level implies that management actions to control the guttural toad should target eggs and tadpoles only when it is possible to fully remove them (Fig. 2); for example, by periodically

draining a pond (Doubledee et al. 2003; Maret et al. 2006) or using chemicals (Campbell and Krauss 2002; Witmer et al. 2015). Under the assumption that fish predation may have strong effects on anuran population dynamics (Schmidt et al. 2021), controlled introductions of native carnivorous fish in garden ponds was also theoretically contemplated as a potential means to decrease guttural toad population size. An analogous approach, based on the use of a native top predatory fish, the northern pike, *Esox lucius*, to control the invasive American bullfrog, *Lithobates catesbeianus*, has been proposed in Belgium (Louette 2012). The lack of selectivity of these techniques may, however, limit their utilisation in the field because they can cause collateral negative effects on non-target populations of anurans, fish and invertebrates (Maret et al. 2006). Recent studies examined the feasibility of introducing species-specific chemical inhibitors of tadpole development into breeding ponds of invasive cane toads, *Rhinella marina* (Beaty and Salice 2013; Clarke et al. 2016). The degree to which the same technique can be utilised in other populations of invasive toads is currently unknown. In light of our study, however, all the above techniques should be used only when their implementation can completely eliminate pre-metamorphic individuals or when management resources allow removing both the most pre-metamorphic and post-metamorphic individuals from all ponds ("successful eradication", Table 2, 3, Fig. 2).

Multiple studies on amphibians have shown that variations in the survival rate of juveniles and sub-adults may have severe population-level effects (Vonesh and de la Cruz 2002; Beaty and Salice 2013; Petrovan and Schmidt 2019; Rose et al. 2021). Therefore, it has been recently suggested that both adults and juveniles of guttural toads should be simultaneously removed (Davies et al. 2020b). However, here we advocate that juvenile removal should never be pursued at the expense of adult removal to control the guttural toad in Cape Town. We observed a considerable discrepancy between the juvenile/adult ratio estimated by captures and the ratio forecast by the model (1:3 and 10:1, respectively). This discrepancy is not surprising, as juvenile amphibians are often more evenly distributed across space and time in comparison with adults which congregate at ponds during breeding periods (Pittman et al. 2014, Table 1). However, we also found that, in our simulation study, an equal removal of 80% juveniles instead of adults from the accessible ponds creates a less severe effect on the population demography (reducing 20% versus 30%, respectively, full data not reported). This contradicts the observation by Govindarajulu et al. (2005) who modelled the management of the invasive American bullfrog and reported the removal of juveniles was more effective than removing an equal number of adults. Adult bullfrogs, however, may cannibalise juveniles and this behaviour was explicitly incorporated in their model. Conversely, toads rarely ingest other anurans (Measey et al. 2015) and this foraging preference makes the demographic impact of such intraspecific interaction negligible in the guttural toad. Given the extremely low capacity to detect and remove juveniles and the limited impact their removal has on adult population size, we do not advocate adopting management strategies, mainly or exclusively, based on the removal of juveniles.

Conclusion

Here, we have shown that the strategy currently adopted to control the invasive guttural toad in Cape Town ensures much greater management efficiency than the strategy initially adopted in 2011. By removing only adults, the implementation team can maximise the reduction of population size without dissipating resources for removal of other stages or causing unwanted consequences, such as those associated with the hydra effect. The management resources, saved by not removing pre-metamorphic individuals, should rather be allocated to increase the proportion of adults that are removed or the spatial scale at which this removal is pursued. Overall, our study demonstrates that simulation models, combining complex population dynamics with management costs and field data, represent valuable tools to guide and improve management decisions for stage-structured invasive populations.

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Supplementary material 1

Supplementary material A
Authors: Giovanni Vimercati, Sarah J. Davies, Cang Hui, John Measey
Data type: Text
Explanation note: Supplementary Material A contains a general description of the stage-structured model used to simulate the population dynamics of guttural toads, *Sclerophrys gutturalis*, in Cape Town.

Link: https://doi.org/10.3897/neobiota.70.72508.suppl1

Supplementary material 2

Supplementary material B
Authors: Giovanni Vimercati, Sarah J. Davies, Cang Hui, John Measey
Data type: Demographic database
Explanation note: Supplementary Material B contains: latitude, longitude, ID and size of the ponds that can be used for breeding by guttural toads, *Sclerophrys gutturalis*, in Cape Town and that have been used in the stage-structured model to reconstruct the guttural toad population dynamics; number of adults occurring in each pond and total adult population size as computed by the stage-structured model simulating different management strategies (Table 2, Fig. 1).

Link: https://doi.org/10.3897/neobiota.70.72508.suppl2