



Effects of learning and adaptation on population viability

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Abstract: Cultural adaptation is one means by which conservationists may help populations adapt to threats. A learned behavior may protect an individual from a threat, and the behavior can be transmitted horizontally (within generations) and vertically (between generations), rapidly conferring population-level protection. Although possible in theory, it remains unclear whether such manipulations work in a conservation setting; what conditions are required for them to work; and how they might affect the evolutionary process. We examined models in which a population can adapt through both genetic and cultural mechanisms. Our work was motivated by the invasion of highly toxic cane toads (*Rhinella marina*) across northern Australia and the resultant declines of endangered northern quolls (*Dasyurus hallucatus*), which attack and are fatally poisoned by the toxic toads. We examined whether a novel management strategy in which wild quolls are trained to avoid toads can reduce extinction probability. We used a simulation model tailored to quoll life history. Within simulations, individuals were trained and a continuous evolving trait determined innate tendency to attack toads. We applied this model in a population viability setting. The strategy reduced extinction probability only when heritability of innate aversion was low (<20%) and when trained mothers trained >70% of their young to avoid toads. When these conditions were met, genetic adaptation was slower, but rapid cultural adaptation kept the population extant while genetic adaptation was completed. To gain insight into the evolutionary dynamics (in which we saw a transitory peak in cultural adaptation over time), we also developed a simple analytical model of evolutionary dynamics. This model showed that the strength of natural selection declined as the cultural transmission rate increased and that adaptation proceeded only when the rate of cultural transmission was below a critical value determined by the relative levels of protection conferred by genetic versus cultural mechanisms. Together, our models showed that cultural adaptation can play a powerful role in preventing extinction, but that rates of cultural transmission need to be high for this to occur.

Keywords: adaptation, conditioned taste aversion, cultural transmission, *Dasyurus hallucatus*, genetic inheritance, population viability analysis, *Rhinella marina*

Resumen: La adaptación cultural es un medio mediante el cual los conservacionistas pueden ayudar a las poblaciones a adaptarse a las amenazas. Un comportamiento aprendido puede proteger a un individuo de las amenazas y este comportamiento puede transmitirse horizontalmente (dentro de las generaciones) y verticalmente (entre generaciones), lo que otorga rápidamente una protección a nivel poblacional. Aunque esto es posible en teoría, aún no está claro si dichas manipulaciones funcionan dentro de un escenario de conservación; cuáles son las condiciones requeridas para que funcionen las manipulaciones; y cómo pueden afectar el proceso evolutivo. Examinamos modelos en los cuales una población puede adaptarse tanto con mecanismos genéticos como culturales. Nuestro trabajo estuvo motivado por la invasión de sapos altamente tóxicos (*Rhinella marina*) en todo el norte de Australia y las declinaciones resultantes de cuoles norteros (*Dasyurus hallucatus*), los cuales atacan y mueren envenenados por los sapos tóxicos. Analizamos si una estrategia de manejo novedoso en la cual los cuoles silvestres son entrenados para evitar a los sapos puede reducir la probabilidad de extinción. Usamos un modelo de simulación diseñado alrededor de la historia de vida de los cuoles. Dentro de las simulaciones, se entrenó a

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cuales individuales y una característica en continua evolución determinó la tendencia innata para atacar a los sapos. Aplicamos este modelo en un escenario de viabilidad poblacional. La estrategia redujo la probabilidad de extinción sólo cuando la heredabilidad de la aversión innata fue baja (<20%) y cuando las madres entrenadas entrenaron a más del 70% de sus crías para evitar a los sapos. Cuando ambas condiciones fueron cumplidas, la adaptación genética fue más lenta pero la adaptación cultural rápida mantuvo a la población vigente mientras se completaba la adaptación genética. Para ganar conocimiento sobre las dinámicas evolutivas (en las cuales vimos un pico transitorio en la adaptación cultural a lo largo del tiempo) también desarrollamos un modelo analítico simple de las dinámicas evolutivas. Este modelo mostró que la fuerza de la selección natural declinó conforme incrementó la tasa de transmisión cultural y que la adaptación procedió solamente cuando la tasa de transmisión cultural estuvo por debajo de un valor crítico determinado por los niveles relativos de protección otorgados por los mecanismos genéticos contra los mecanismos evolutivos. En conjunto, nuestros modelos mostraron que la adaptación cultural puede jugar un papel importante en la prevención de la extinción, pero las tasas de transmisión cultural necesitan ser altas para que esto ocurra.

Palabras Clave: adaptación, análisis de viabilidad poblacional, aversión al gusto condicionado, herencia genética, transmisión cultural, *Dasyurus ballucatus*, *Rhinella marina*, 适应, 条件性味觉厌恶, 文化传播, 北方袋鼯, 遗传, 种群生存力分析, 海蟾蜍

摘要: 文化适应是保护主义者帮助种群适应威胁的一种手段。后天习得行为可以保护个体免受威胁,且这种行为可以横向(代际内)和纵向(代际间)传播,迅速实现种群水平的保护。尽管这种方法在理论上是可行的,但人们尚不清楚此类操纵在保护的情境中是否有效、需要什么条件,以及将如何影响演化过程。本研究检验了种群可通过遗传和文化机制产生适应的相关模型。我们的工作源自于具有剧毒的海蟾蜍(*Rhinella marina*)在澳大利亚北部的广泛入侵和由此导致的濒危物种北方袋鼯(*Dasyurus ballucatus*)的种群下降,这些袋鼯会攻击毒蟾蜍并被它们毒死。我们研究了训练野生袋鼯躲避蟾蜍的新管理策略是否可以降低袋鼯的灭绝概率。我们按照袋鼯的生活史设计了一个模拟模型,其中,个体会接受训练,并由一种持续演化的特征来决定其攻击蟾蜍的天性。我们将这个模型应用于种群生存力检验中,发现仅在先天的对蟾蜍厌恶的遗传率低(<20%)及受训母袋鼯训练70%以上的后代躲避蟾蜍的情况下,该策略可以降低袋鼯的灭绝概率。当满足这些条件时,遗传适应较慢,但快速的文化适应保证了种群存活至完成遗传适应。为了深入了解演化动态(我们发现演化过程中文化适应出现过短暂峰值),我们还开发了简单的演化动态分析模型。该模型表明,自然选择的强度随着文化传播率的增加而下降,且只有当文化传播率低于临界值时适应才能继续,而该临界值由遗传机制与文化机制形成的保护的相对水平所决定。总之,我们的模型表明,文化适应可以在防止物种灭绝中发挥重要作用,但需要文化传播率足够高才可以实现。【翻译:胡怡思;审校:聂永刚】

学习和适应对种群生存力的影响

Introduction

Global extinctions represent a failure of many species to adapt to the rapid environmental changes wrought by humans. Anthropogenic impacts are extremely difficult to mitigate at a landscape scale (Barnosky et al. 2012), so in most cases populations must adapt to rapidly changing circumstances or go extinct. How might conservationists speed the rate at which populations adapt to known threats?

Although evolutionary adaptation can proceed quickly under the right circumstances, cultural adaptation has the potential to proceed more rapidly still (Cavalli-Sforza & Feldman 1983). Under a cultural model, lessons learned during an individual's lifetime can be transmitted to its conspecifics and offspring (Sheppard et al. 2018). If the lesson is relevant to a threatening process and if it is transmitted with sufficient fidelity, cultural evolution may allow populations to adapt to novel circumstances very rapidly. Although learning and cultural transmission are regularly observed in a wide array of taxa (McComb et al. 2001; Whitehead & Richerson 2009), only rarely has

that possibility been explicitly incorporated in models of population viability (Whitehead 2010). Rarer still (and possibly nonexistent) are models that incorporate both genetic and cultural adaptation that ask how these 2 processes may interact and affect conservation outcomes. We developed such a model explicitly motivated by a real situation—cane toads (*Rhinella marina*) and northern quolls (*Dasyurus ballucatus*) in northern Australia—to examine the conditions under which cultural adaptation may generate positive outcomes and how evolutionary adaptation is affected by cultural dynamics.

In Australia conditioned taste aversion (CTA) has gained attention as a potential conservation tool to train vulnerable animals to avoid toxic invasive cane toads (O'Donnell et al. 2010; Ward-Fear et al. 2016; Cremona et al. 2017a; Jolly et al. 2018). Conditioned taste aversion involves pairing the consumption of a food item (e.g., a small toad) with a nauseating experience (typically by administration of a drug such as thiabendazole). The resultant illness is strongly associated with the referent food, and that food is avoided for some time thereafter (Garcia et al. 1985). Most Australian predators have no

evolutionary history of exposure to toads and so are extremely sensitive to the defensive toxins in toad skin (Phillips et al. 2003; Smith & Phillips 2006; Ujvari et al. 2013). In an attempt to minimize the impact of toads, vulnerable native Australian predators, ranging from lizards to predatory marsupials, have been successfully trained via conditioned taste aversion to avoid eating cane toads (e.g., Indigo et al. 2018; Jolly et al. 2018; Ward-Fear et al. 2016). Northern quolls are one such predator. Using CTA, individual quolls can be successfully taught to avoid toads as prey (O'Donnell et al. 2010). Radiotelemetry and mark-recapture studies demonstrate that some of these toad-trained quolls can survive (Jolly et al. 2018) and reproduce when introduced to the wild and their offspring can survive in toad-infested landscapes (Cremona et al. 2017a, 2017b). Although it is clear quolls can be trained, it is still unknown whether wild-born quolls can be taught to avoid toads by their toad-smart mother (via cultural transmission). Although most quoll populations are extirpated upon the arrival of toads, several populations show clear evidence of genetic adaptation: offspring are born with a tendency to avoid toads as prey (Kelly & Phillips 2017, 2019a). The fact of genetic variation for toad-smart behavior makes it unclear whether the apparent intergenerational persistence in CTA-manipulated populations (Cremona et al. 2017a, 2017b) is driven by cultural or genetic transmission. More broadly, it remains unclear how best to speed the rate at which quoll populations adapt. What are the conditions under which a CTA-driven cultural shift may help, and would a cultural response slow the rate of genetic adaptation?

Regardless of broader questions around cultural adaptation, projecting the trajectory and likely outcome of a novel conservation strategy, such as CTA training, is an important exercise for conservation practitioners. In this regard, population viability analysis (PVA) is useful for scenario testing (Boyce 1992; Brook et al. 2000). Modeling can provide guidance for successful delivery of management techniques within complex biological systems, saving time and money (McLane et al. 2011; Bode & Brennan 2011; Restif et al. 2012). A recently developed evolutionary model (Kelly & Phillips 2019b) allows for genetic adaptation and has already been customized to describe the quolls' life history and evolutionary response to toads. We added the possibility of rapid learning and cultural transmission to that model and used it in a PVA framework to determine the conditions under which CTA might enable quoll populations to adapt to the presence of toads. Against a model in which the population evolves, we specifically examined the robustness of CTA for preventing population extinction under scenarios in which we varied efficacy of the initial CTA training (i.e., proportion of the population successfully trained to avoid toads) and vertical transmissibility of the CTA lesson (i.e., ability of females to pass the lesson on to their offspring).

Table 1. Initial values for the additive genetic and environmental variances included in the current model (adapted from Kelly and Phillips [2019b]).

Parameter	Notation	Initial value
Heritability (of the toad smart trait in the recipient population)	b^2	0.2
Total phenotypic variance	V_T	1
Initial fitness	W_0	0.38
Initial frequency of favorable alleles	f_0	0.05

Methods

For the PVA, we used the discrete-time, individual-based population model described in Kelly and Phillips (2019b). The model was customized to reflect the life history of quolls and contained a simple quantitative genetic model, allowing for the evolution of a continuous trait that, once beyond a threshold value, confers toad-smart behavior on an individual. The initial additive genetic and environmental variances are identical to those used by Kelly & Phillips (2019b) (Appendix S1). The complete description of the model (including code) is available in Supporting Information (Appendix S1), on GitHub (<https://github.com/benflips/CTAquolls>), and in Kelly and Phillips (2019b). The model is motivated by empirical observations that a proportion of the quoll population is innately toad smart and that this trait is heritable (Kelly & Phillips 2017, 2019a) (Table 1). Given this heritability and initial proportion of toad smarts, the modeled population evolves in response to the arrival of toads, increasing the proportion of toad smart individuals in the population over time. Despite the population's capacity to evolve, it is often extirpated before adaptation is complete—a result echoed in wild quoll populations exposed to toads (Woinarski et al. 2010). We extended this model to incorporate the capacity for quolls to learn toad avoidance (see Appendix S1).

Our extension of Kelly & Phillips' (2019b) model incorporates two extra parameters to describe the efficacy with which the one-trial CTA lesson is imparted to wild quolls in a single training effort, E (describing the proportion of the toad-susceptible population that is effectively trained) and the probability of cultural (vertical) transmission of the CTA lesson—from mother to offspring— T (Fig. 1). We ignored horizontal transmission—from one individual to another within a generation—because we considered this unlikely in this solitary foraging species. Although CTA training occurs only once, at the beginning of simulations, the training propagates forward in time as females train their offspring with probability T . Individuals born to culturally toad-smart mothers inherit this characteristic from their mothers with probability T whether or not they are also genetically smart. Thus, beyond the initial training generation, it is possible for an animal to be both genetically and culturally adapted.

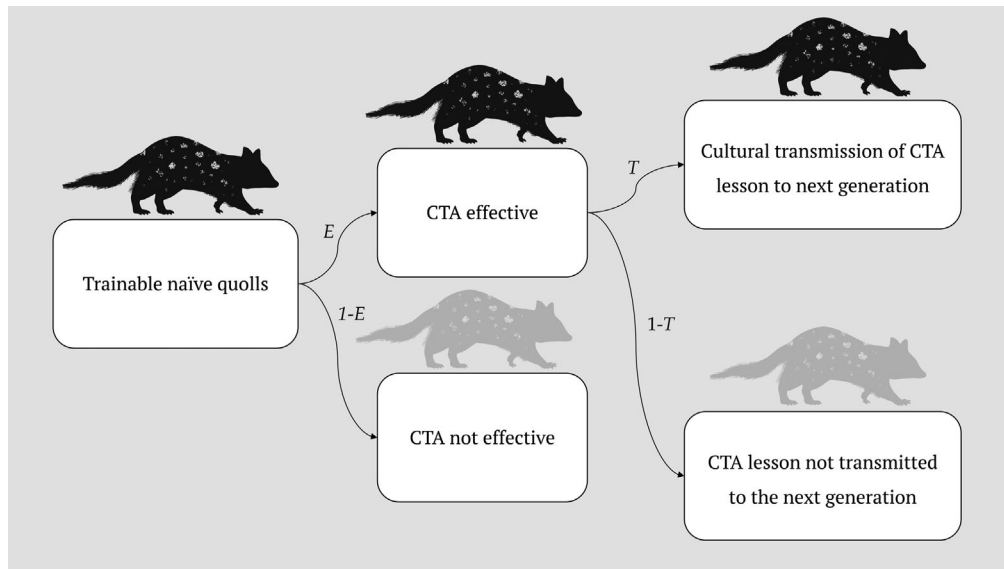


Figure 1. Incorporation of the capacity for quolls to learn toad avoidance through conditioned taste aversion (CTA) with 2 extra parameters (E , efficacy with which the 1-trial CTA lesson is imparted to wild quolls; T , probability of cultural transmission of the CTA lesson) added to the Kelly and Phillips' (2019b) model. Genetically toad-smart quolls are untrainable (they will not take baits), so only the trainable portion of the population is considered here. Bifurcation occurs when trainable quolls effectively learn a CTA lesson (E) or fail to learn ($1 - E$). The second bifurcation for trainable quolls occurs when the CTA lesson is transmitted culturally (T) or not transmitted ($1 - T$).

Our base scenario considered a carrying capacity (K) of 1000 individuals (though we also ran a set of scenarios with $K = 100$), and we initiated our scenarios with an initial fitness (W) of 0.38, which is the observed proportion of animals that would not take cane toad baits in the field and are, thus, likely to exhibit an innate (genetically based) aversion to consuming cane toads (Indigo et al. 2018; Kelly & Phillips 2019a). The genetic heritability of this toad-smart behavior is unknown; although as with many behavioral traits, it likely ranges from 0.1 to 0.3 (Kelly and Phillips 2019b; Roff 2012). We explored outcomes across heritabilities from 0 to 0.5.

We explored CTA under several scenarios. First, we examined CTA efficacy—with no cultural transmission between generations ($T = 0$). Following this we explored the possibility of CTA with differing levels of T , from 0 to 1 (0, no transference; 1, perfect transference) in increments of 0.1, and E , from 0 to 1 in increments of 0.1, over 50 generations. In each case we investigated how these parameters influenced extinction probability (estimated over 100 simulations per parameter set). In each scenario, we recorded whether the population went extinct or not over 50 years following the arrival of cane toads. We also recorded the mean phenotype of populations persisting through 50 years to observe whether persistence was driven by genetic or cultural shifts (or both). Model simulations were implemented in *R* (R Core Team 2019).

We used survival estimates that differed by sex and age from Begg (1981), Braithwaite and Griffiths (1994), Oakwood (2000), and Schmitt et al. (1989) (see Appendices S1 and S2). We updated these with recent survival values estimated using data collected during a 6-year mark-recapture study across multiple sites in the Kimberley, Western Australia (Appendix S2). Recent survival estimates from the Pilbara (Hernandez-Santin et al. 2019) were not included in our PVA model because the Pilbara populations are genetically distinct with a demonstrably different life history (reproduction occurs at a different time of year and semelparity is incomplete). The input values along with the information source for the model are in Appendix S2.

Results

Population Viability

Extinction probability decreased rapidly as genetic heritability (b^2) increased (Fig. 2), as would be expected by the more rapid evolutionary response facilitated by higher heritability. Cultural adaptation (CTA) reduced this baseline probability of extinction only when the efficacy of training (E) was >0 and the transmissibility (T) of the lesson between generations was >0.7 (Fig. 2b-d). When $E > 0.2$ and $T > 0.7$, the probability of extinction began to fall below the reference case of $E = 0$ (Fig. 2b).

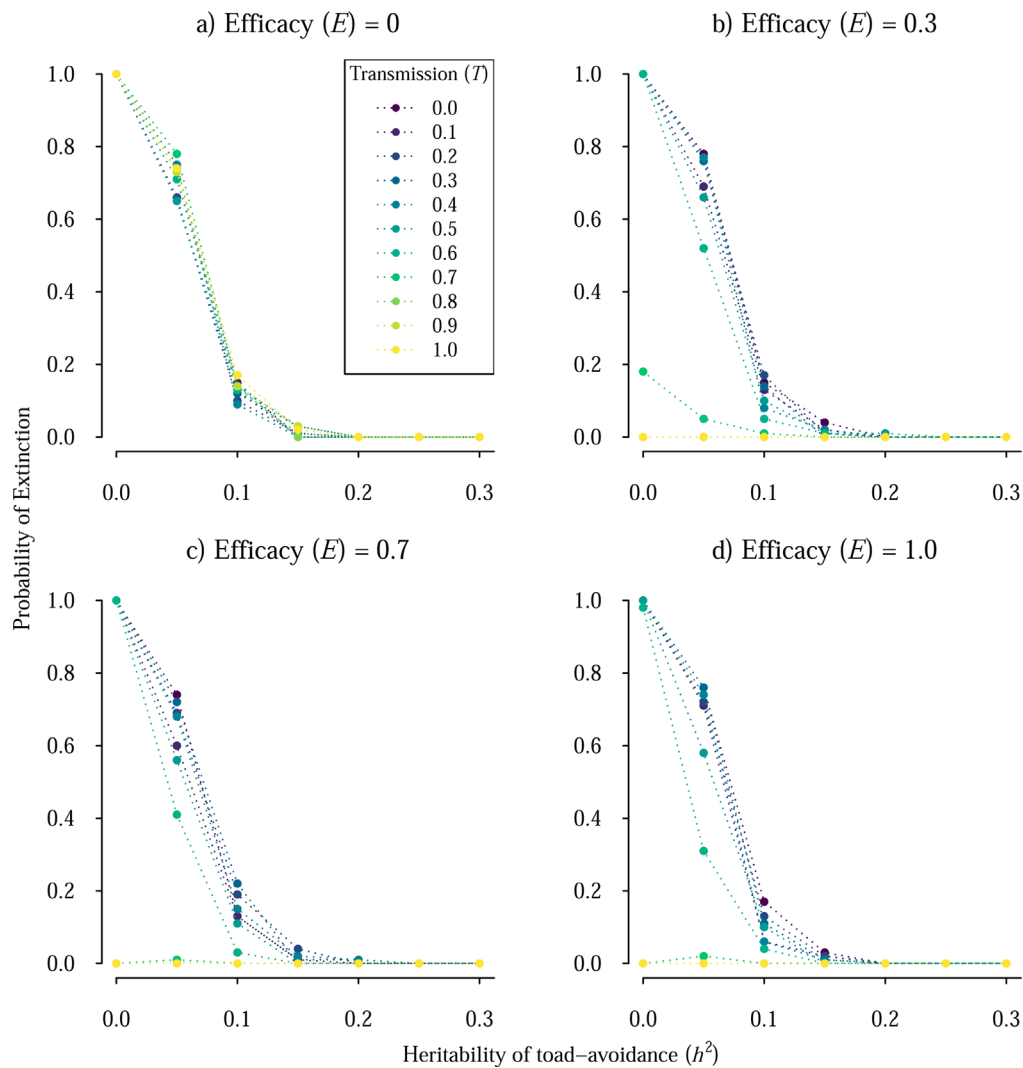


Figure 2. The effect of efficacy (E) and transmissibility (T) of a cane-toad-conditioned taste-aversion lesson and its interaction with the genetic heritability (h^2) of toad-avoidance traits on the extinction probability of a population of northern quolls. When (a) $E = 0$ (baiting fails to train quolls), population viability is solely dependent on the genetic heritability of innate toad avoidance in the population. In all other scenarios (b-d), when $E > 0$, the probability of population extinction is also influenced by the transmission of learned toad-avoidance information from mother to offspring. When heritability of genetically acquired toad-avoidance behavior is low ($h^2 < 0.2$) (b-d), high levels of cultural transmission ($T > 0.7$) can substantially reduce the likelihood of extirpation.

Genetic Versus Cultural Adaptation

Our model also revealed a clear interaction between genetic and cultural adaptation. In the absence of cultural adaptation ($E = 0$) (Fig. 3a), the population either evolved successfully or was extirpated. With no cultural adaptation and low heritabilities ($h^2 < 0.1$ when $E = 0$), the population always went extinct, so we could not measure final phenotypes. By contrast, when $E = 1$ and $T = 1$, the population adapted through purely cultural means, and the proportion of genetically adapted animals did not shift far from its initial value of 0.38, a result almost completely unaffected by the heritability of the trait (Fig. 3d & 4). Below this case of complete cul-

tural transmission (i.e., $T < 1$), the population ultimately reached complete genetic adaptation, although the rate of genetic adaptation was slowed substantially by higher cultural transmission rates (Fig. 3).

It remains possible that the frequency of genetically adapted animals in the population after 50 generations did not represent the equilibrium frequency. To test this possibility, we examined a longer iteration time for the case in which $E = 1$ and $h^2 = 0.3$. When we examine this scenario over 200 generations (Fig. 4), the above observations appeared to reflect true equilibria rather than transitory states. We also saw that genetic adaptation proceeded in a steady monotonic increase over time

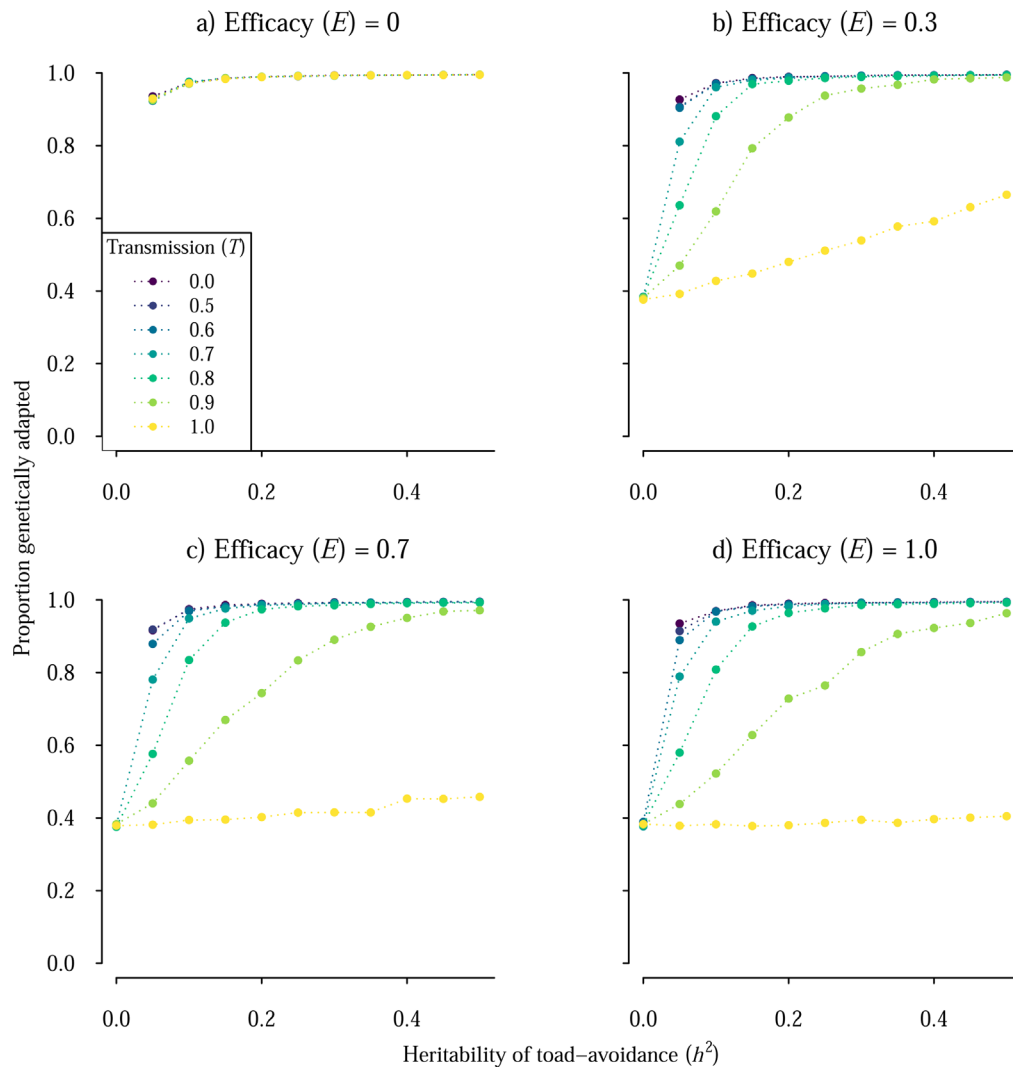


Figure 3. The effect of cultural adaptation on genetic adaptation of toad avoidance in a population of northern quolls (points, proportion of genetically adapted individuals in populations extant at the end of simulations).

(Fig. 4a). By contrast, in the high-transmission scenarios in which extinction probability was reduced ($T > 0.7$), the proportion of cultural adaptation had an intermediate peak before it declined to 0 (Fig. 4b). It appeared that the reduction in extinction probability effected by cultural transmission was associated with a transitory increase in the proportion of culturally adapted individuals.

Evolutionary Dynamics with a Simple Analytic Model

Our simulation model was complex. On the one hand, a polygenic trait exhibited stochastic environmental variation and incomplete heritability. On the other hand, we had a fully parameterized life-history model of a semelparous mammal. Nonetheless, quite simple evolutionary dynamics emerged, and one might gain clear insight into these through a much simpler analytical model. To this

end, we considered the simplest possible model: a population of haploid individuals evolving in discrete time in an exponentially growing population of very large size with nonoverlapping generations. We considered a single locus in which allele A confers resistance and allele a confers susceptibility to toads. Alleles do not affect reproductive fitness, but they have complete effects on survival in the presence of toads.

We commenced with a polymorphic population at the time toads arrived, and we needed to track numbers of three classes of individuals: those carrying the resistant A allele (n_A); those carrying the susceptible a allele that were toad smart through cultural means (n_{a+}); and those carrying the a allele that were not toad smart (n_{a-}). Births per individual (b) were identical across our 3 classes, and the probability of death (d) was identical between A and $a+$ individuals and equal to 1 for the $a-$ individuals. A proportion, T , of $a+$ individuals' offspring successfully

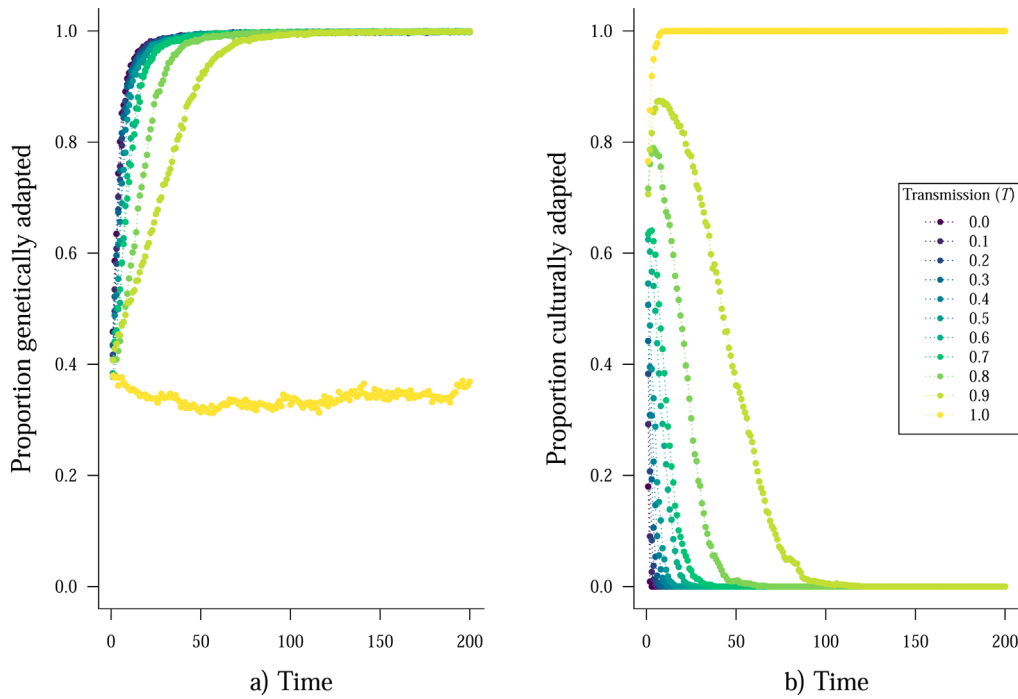


Figure 4. The proportion of the quoll population genetically and culturally adapted over time at varying rates of cultural transmission (T) of toad-avoidance behavior. An individual can be both culturally and genetically adapted, so these 2 proportions do not sum to 1. Each point represents the mean of 10 simulation runs at the particular value of T and $E = 1$ and $h^2 = 0.3$ in all runs.

received cultural transmission from their parent (with $1 - T$ failing and so changing to $a-$). Following birth, training, and death in that order, we found the following recursions over time (t):

$$n_A(t + 1) = b(1 - d)n_A(t)$$

$$n_{a+}(t + 1) = bT(1 - d)n_{a+}(t), \text{ and} \quad (1)$$

$$n_{a-}(t + 1) = 0.$$

These indicated that only numbers of n_A and n_{a+} needed to be tracked because all $a-$ individuals were killed each generation and their only source were $a+$ individuals that had failed training. We ignored $a-$ individuals and set

$$p(t) = \frac{n_A(t)}{n_A(t) + n_{a+}(t)} \quad (2)$$

This allowed us to express our dynamics as a recursion on a single variable, p :

$$p(t + 1) = \frac{p(t)}{p(t) + T(1 - p(t))} \quad (3)$$

At which point, our system was identical to classic models of natural selection (Crow & Kimura 1970), with T describing the relative fitness between A and a alleles.

We needed go no further to determine whether when $T < 1$, p would run to a stable equilibrium of 1. When $T = 1$, the system was at equilibrium, regardless of its current state: $p(t+1) = p(t)$.

Viewing our system as a simple model of natural selection also yielded further insights. For example, when we relaxed our assumption of equal death rates and instead allowed class-specific rates, d_A and d_{a+} , while still fixing d_{a-} at 1, it was clear that the proportion genetically adapted p increased only when

$$T < \frac{1 - d_A}{1 - d_{a+}} \quad (4)$$

Thus, when genetic adaptation yielded only partial protection relative to cultural adaptation, cultural adaptation could be the stronger strategy and run toward fixation. It is difficult to translate this result to our simulation results because in our simulation, d_A itself evolved, but it nonetheless provided insight into how one might achieve transient increases in the proportion of cultural adaptation (Fig. 4). The polygenic nature of our modeled trait (plus recombination) meant that genetically resistant individuals could still produce offspring that were susceptible, so in this sense genetic adaptation only gave partial protection. In our simulation, initially, our population was poorly adapted, $\frac{1 - d_A}{1 - d_{a+}} \approx 0.38$, but selection rapidly caused d_A to drop, and so this value increased over time. Eventually, the trait value

shifted far enough that genetically resistant individuals produced very few susceptible offspring, at which point the proportion of culturally adapted individuals in the population started to drop. If this interpretation is correct, then the cultural response would last longer and be stronger if the evolutionary response were slowed by reducing heritability in the model, an effect our simulations showed (Fig. 4).

Discussion

We asked whether cultural adaptation might provide an additional, potentially faster, mechanism for adaptation, beyond that provided by evolution. If populations can adapt through both genetic and cultural mechanisms, is the probability of extinction reduced? This question is general, but our results with quolls and cane toads imply that it is indeed possible for cultural response to reduce extinction probability. But, this occurred only under very specific conditions in our simulations: when learning provided a large improvement in fitness and when cultural transmission rates were high. Our results also showed that cultural adaptation can slow, halt, or even (in our analytic model) reverse the evolutionary response that would occur in the absence of cultural effects. In both our simulation and analytic models, perfect cultural transmission stopped the evolutionary process entirely by removing selection.

We examined a very real conservation action. Conservation agencies in northern Australia are deploying baits and teacher toads in an attempt to train naïve native predators to avoid consuming toads. The hope is that, when toads arrive, a proportion of the susceptible quoll population will have been trained, will thus avoid poisoning themselves with a toad, and so will survive and go on to reproduce. Our PVA revealed that, even if all toad-susceptible individuals are trained in the first generation ($E = 1$), there is no benefit to the population unless there are high rates of cultural transmission. Unless the lesson is passed on to offspring, the initial training effort simply reduces initial mortality. In doing so, training also reduces the strength of natural selection on the population (some animals survive that otherwise would have died). The full impact of toads is simply delayed by one generation. And over 50 generations, this delay matters not at all to the probability of extinction. Further scenarios were also explored varying the efficacy (E) of the initial CTA training and the rate of cultural transmission (T) of the CTA lesson. Importantly, when heritability was low, $E > 0.2$, and $T > 0.7$, the probability of extinction decreased substantially (Fig. 2b). At high levels of T (i.e., $T > 0.8$), the probability of extinction was near zero and was largely independent of the heritability of toad-averse traits. At slightly lower levels of T and with low heritability ($b^2 = 0.2$), even moderate levels of E of CTA

significantly decreased the extinction probability. These positive outcomes are encouraging but depend on a high cultural transmission rate (i.e., mothers teaching young), for which there remains no evidence in quolls. In other toad-affected taxa for which CTA is being trialed, such as reptiles, there is no maternal care of hatchlings and so no chance for cultural transmission. In the absence of high cultural transmission rate, our models showed that population persistence relies entirely on natural selection acting to select for innate, heritable aversion of toads (Kelly & Phillips 2017).

From a pragmatic perspective, managers are likely to be agnostic about how adaptation is achieved, as long as the population remains extant. But the interplay between cultural and genetic adaptation is, nonetheless, interesting, and we found that when conditions favored rapid cultural response (high efficacy and transmissibility), the evolutionary response was slowed. Our analytic model showed that this occurred because cultural transmissibility was the complement of selection in our system: higher transmissibility equaled lower selection against genetically maladapted variants. Our results also showed that cultural effects may play a much more important role in situations where key traits have low heritability. Here, the adaptive response was slow because natural selection had little genetic variation to work with; cultural responses can be much more rapid. These cultural responses further slowed the evolutionary response, but in the meantime, the strong cultural response prevented the population from being extirpated. Thus, while the ultimate outcome was still genetic adaptation, cultural effects kept the population extant while it adapted.

Cultural transmission of information between individuals has been observed in many species and could well enable species to adapt rapidly to environmental change (Whitehead et al. 2004; Thornton & Raihani 2008, 2010). Cultural transference of an acquired lesson—such as a food preference and avoidance—is transmitted through peripheral cues to conspecifics and offspring. This occurs by either observing demonstrators (Thornton & Clutton-Brock 2011; Hoppitt & Laland 2013) or through active teaching, where a demonstrator may jeopardize its own fitness to facilitate the learning of a naïve animal (Thornton & Raihani 2010). An animal relies heavily on peripheral cues during active teaching (Gustavson et al. 1974; Brett et al. 1976), and these cues develop as a result of early learning, experience, interactions with the environment, genetic predispositions, food availability, and the feeding preferences of adults (Lindström et al. 1999; Francis et al. 2003; Mappes et al. 2005). Although offspring may readily learn from others which foods to eat, it is much less clear that they learn from others which foods to avoid eating (Galef 1989; Galef & Giraldeau 2001; Dewar 2004). Rigorous experimental data to support or reject the possibility that a CTA lesson

might be passed on to offspring is extremely challenging to collect. Obtaining this information for a nonmodel and endangered species, such as the northern quoll, renders this an exceptionally difficult challenge.

It is, however, possible that adult quolls that receive CTA training could teach their offspring to also avoid eating cane toads. Juvenile quolls may learn what to eat and what not to eat by copying the food preferences of their mothers. Prior to dispersal, juvenile quolls spend a significant period foraging with their mothers (Cremona 2015) and, like other mammals, they may learn to eat palatable foods and avoid unpalatable foods simply by observing their mothers' food choices (Mirza & Provenza 1990; Galef & Giraldeau 2001). Unfortunately, evidence suggests they are not tightly bound to food preferences or avoidances based purely on what they have observed their mothers eating and avoiding during development. Northern quoll conservation efforts have seen at least 100 quolls brought from the wild into captivity for captive breeding and CTA training. In captivity wild-caught quolls readily take to a completely novel diet composed of foods they would have never encountered with their mothers during development or during their evolutionary history in the wild (e.g., dog kibble, chicken necks, pilchards, grapes). In fact, in some instances, northern quolls collected from Queensland that have a demonstrably evolved aversion to cane toads (Kelly & Phillips 2017, 2019a) and would likely have observed their mothers avoiding toads during their development, learned to eat sublethal toads in captivity despite being unwilling to eat toads on arrival (Appendix S3). A study from Kakadu National Park showed that some female quolls subjected to CTA treatment and reintroduced into toad-infested areas survived and reproduced and that their offspring also survived and reproduced (Cremona et al. 2017b). Although parentage analyses determined that some of animals persisting in this landscape were the offspring of CTA-trained females, wild, untrained male quolls, which potentially possessed a genetic aversion to toads, existed in this population and would likely have fathered most of these young. Thus, although toad aversion was likely passed onto offspring from a parent, it is impossible at this stage to determine whether genetic or cultural transmission (or both) was responsible for this transference of information between generations (Cremona et al. 2017b).

Our results suggest that without the transmission of toad aversion between generations, CTA alone is unlikely to allow quoll populations to persist following the arrival of cane toads. There is, however, an additional mechanism involved in landscape-scale CTA that may provide some indirect protection to toad-vulnerable species. The toad invasion front is dominated by large, fatally toxic cane toads (Phillips et al. 2010) that rarely reproduce (Hudson et al. 2015), resulting in juvenile, sublethal toads being extremely scarce during the initial invasion

period (Brown et al. 2013). It has been proposed that if CTA can delay the impacts of toads even by a single generation until small, sublethal toads are present in the population, this may give the offspring of CTA trained animals an opportunity to learn to avoid cane toads in the wild, by encountering small, sublethal toads (teacher toads) rather than adult toads. It is argued that this might be a mechanism through which CTA training could offer longer-term toad protection to other toad-vulnerable animals, such as goannas (*Varanus* sp.), where cultural transmission is extremely unlikely (Ward-Fear et al. 2016, 2017; Tingley et al. 2017). We know, however, for quolls at least, the presence of small, sublethal toads in the environment does not necessarily mean predators will encounter a training opportunity before a fatal toad interaction. In fact, this has been indirectly tested by reintroductions of toad-naïve quolls into areas composed of mature toad populations with the full breadth of size classes present. In two introductions of toad-naïve quolls to toad-exposed landscapes, the vast majority of untrained quolls were killed within days because they attacked lethal-sized toads (O'Donnell et al. 2010; Jolly et al. 2018). We also have the sobering observation (above) of toad-averse quolls slowly learning to eat toads when regularly offered small, sublethal toads. These 2 observations can be explained by the simple fact that the therapeutic window for toad toxin is very narrow: a small dose may have little to no observable effect, but a slightly larger dose will kill (e.g., Phillips et al. 2003; Smith & Phillips 2006). Thus, there is little room for learning through experience. Although learning experiences from toads have been observed in experimental settings (reviewed in Brown [2013]), it is less clear that they occur in natural settings. Learning experiences are theoretically possible in a landscape where small toads are present, but for many predator species the relevant toad size classes will often be rare or only briefly present in any year.

Our simulation model showed that the deployment of toad-aversion baits could help mitigate the impact of cane toads on northern quolls, but to do so it would require high cultural transmissibility and a moderately effective initial CTA training effort. While high CTA training efficacy (i.e., bait uptake by a high proportion of the population) is possible to achieve (Indigo et al. 2019), populations will go extinct very rapidly if high efficacy is not achieved (Indigo 2020). Beyond this first year, the ongoing value of CTA manipulation depends critically on the transmission of toad aversion between generations, a variable for which we have very little information. If adequate cultural transmission does not occur in this species, managers would be well advised to focus on evolutionary means of reducing the vulnerability of toad-affected species (e.g., targeted gene flow) (Kelly & Phillips 2019a,b). More broadly, our results provide a cautionary conservation message, individual-level

conservation benefits are often assumed to scale up to population- or species-level protections; however, this assumption should be tested wherever possible because it is clearly not inevitable.

Overall, we found that cultural adaptation may provide a rapid and powerful route by which a population could adapt to rapid change, but only if rates of cultural transmission are very high. Cultural transmission rate was the key variable affecting outcomes. If cultural transmission is perfect, a population could adapt very rapidly without any concurrent genetic shift. Where cultural transmission is slightly less than perfect, rapid cultural adaptation followed by a slower adaptive response in the genome may occur because imperfection in transmission translates directly into selection pressure on the genes affecting fitness. Where cultural transmission is poor, cultural adaptation plays little to no role in reducing extinction probability. Although cultural transmission reduces selection and so slows the genetic response, it also reduces the demographic impact of environmental shift and in some circumstances can allow the population to persist while genetic adaptation plays out.

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Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. All simulations and plotting code are available from GitHub (<https://github.com/benflips/CTAquolls>).

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