Toad invasion of Malagasy forests triggers severe mortality of a predatory snake

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Abstract

The Asian common toad *Duttaphrynus melanostictus* has been introduced to the eastern province of Toamasina in Madagascar, where it is feared to be having devastating effects on native communities by poisoning frog-eating predators. So far it was unclear whether the toad can invade forest habitats, and empirical evidence of its impact on native predators was lacking. We used radio tracking to investigate the spatial behaviour of adult toads in a small parcel of lowland humid forest and we quantify the disruptive effects of toad poisoning on a native frog-eating snake, the Malagasy cat-eyed snake (*Madagascarophis colubrinus*). We used *N*-mixture models to estimate the population size of cat-eyed snakes, and used the mortality events recorded in the same area to obtain an estimate of monthly mortality rate of snakes due to toad poisoning. Our results point to severe mortality rate of snakes that, if constant through the year, could halve the predator population, with the potential risk of extirpation. We expect cat-eyed snake populations across rural and suburban areas of Toamasina to be severely affected by the toad invasion, and suggest that future research should investigate the effects of indirect facilitation of human-commensal rodents and the potential repercussions on human health and well-being.

Keywords: toad poisoning, *Duttaphrynus melanostictus*, Malagasy cat-eyed snake, *N*-mixture models, mortality rates

Declarations

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Introduction

Madagascar is one of the richest biodiversity hotspots hosting some of the most irreplaceable forests on Earth (Le Saout et al. 2013), where, until recently, invasive species have received only limited attention (Kull et al. 2015). This paradigm is rapidly shifting since the introduction of the Asian common toad (*Duttaphrynus melanostictus*) (VII IUCN World Conservation Congress 2020). Likely having arrived around 2010, the Asian common toad rapidly established in urban and suburban areas of the seaport town of Toamasina (eastern Madagascar) (Andreone et al. 2014; Crottini et al. 2014; Kolby et al. 2014), where it is now relentlessly spreading through rural habitats. Recent estimates report an incursion area of over 500 km^2 and an average spread rate of 2.5 km per year (Licata et al. 2019); complete eradication is therefore highly unlikely (Licata et al. 2020). This toad can reach high abundances in human-dominated habitats, which likely facilitated the establishment of the species in the initial stages of the invasion (Licata et al. 2019, 2020). Invasive toads can affect naïve native communities both by directly affecting specific species or populations, and by disrupting trophic interactions through bottom-up (prey limitation) or top-down (predator removal) effects (Kraus 2015). The invasion of this species in Madagascar represents an unfortunate parallel with the infamous cane toad (*Rhinella marina*) invasion of Australia, which has caused severe declines of several predators, thereby generating trophic cascade effects on Australian ecosystems (Shine 2010). Although the invasion of Asian common toads in Madagascar has received recent attention (Moore et al. 2015; Vences et al. 2017; Marshall et al. 2018; Licata et al. 2019, 2020), studies measuring pathways of ecological and socio-economic impact are lacking (Licata et al. 2020).

The major risk of this invasion lies in the toxicity of the toads, and on the predicted widespread vulnerability of the native vertebrate fauna to their toxins, with predator removal due to poisoning being the most feared effect (Marshall et al. 2018). As mesopredators, snakes may play a crucial role in the maintenance of ecosystem functioning and are particularly exposed to the effects of the current biodiversity crisis (Zipkin et al. 2020). In Madagascar, several snake species are specialized to feed on lizards and amphibians (Andreone and Luiselli 2000), probably due to the great availability of these taxa in Malagasy rainforests, and may therefore be at risk of ingesting the toxic toads.

The magnitude of this impact is likely dependent on the ability of toads to colonize rainforests (Marshall et al. 2018), where the abundance of frog-eating predators (e.g., snakes) is the highest (Glaw and Vences 2007). In this study, we explicitly show that the invasive toad is able to colonize densely forested habitats and quantify for the first time the impacts of toad poisoning on an endemic frog-eating snake.

Methods

Study site

Analabe, located about 6 kilometers west of the seaport town of Toamasina (18°6'18.31''S, 49°19'23.32''E, around 40 m a.s.l.), is one of the few remnant patches of lowland humid forest that survived recent slash-and-burn activities in the region (Fig. 1a, b).

This forest fragment covers an area of approximately 17 ha and is characterized by dense but degraded native vegetation with a temporary pond in the central area. This site is included within the Asian common toad incursion, and was probably reached by the toad between 2014 and 2016 (Licata et al. 2019). Climatic conditions in the region are characterised by a tropical rainforest climate (Peel et al. 2007), alternating between a drier period (August–November) and a wet season (December–July), with monthly temperatures ranging from 21°C (July) to 27°C (February) (Merkel 2021).

Despite being small, Analabe harbors a remarkably rich herpetofaunal community, with at least 18 species of native amphibians and 16 species of native reptiles.

Field investigations were performed from 16 November 2018 to 21 February 2019, and from 23 April to 18 May 2019. We conducted regular surveys in multiple areas of the forest, starting soon after dusk, searching for active toads using headlamps.

Radiotelemetry of Duttaphrynus melanostictus

Between 23 November 2018 and 12 February 2019, eight adult Asian common toads (n = 2 males; mean ± SD; SVL = 74.5 ± 3.5 mm, mass = 30.6 ± 2.8 g; n = 6 females, 75.8 ± 3.1 mm, 38.7 ± 5.9 g) were found within or in close proximity to the edges of the forest. We fitted flexible belts around their waists (each belt made of silicone rubber capillary tubing of ca. 0.05 g) (Alford and Rowley 2007) holding a radio-transmitter (mass = 2.5 g; model NTF-6-1; Lotek Systems, Ontario, Canada) which weighed less than 10% of the toads' mass (Richards et al. 1994) and did not limit their movements. Toads were released at the capture site within the following 24 hours.

To investigate the spatial behaviour and microhabitat use of adult toads, we tracked toad positions both during the day and at night, aided by a receiver and hand-held Yagi antenna (White and Garrott 1990). We recorded GPS locations (Garmin GPSMAP60 CSx; Garmin, Kansas, USA), type of shelter and activity status. The tracking period was on average 12.4 days (range = 5–21 days), and toad locations were obtained every 1 to 7 days (median = 3 days). Using the GPS points, we calculated the average distance between successive locations, the range span (i.e., the distance between the furthest positions recorded), and the Minimum Convex Polygons (100 % of locations), to obtain the extent of distribution of locations.

Snake Abundance Estimates

After detecting the first Malagasy cat-eyed snake (*Madagascarophis colubrinus*; hereafter cat-eyed snake) carcass, we hypothesized that the most likely cause of death was ingestion of toad toxins, and considered cat-eyed snakes to be at risk of mortality where toads are present.

To estimate the abundance of cat-eyed snakes, we surveyed approximately 1,350 m^2 of Analabe. The area was surveyed through regular inspection of five 150 m-long transects in the dense vegetation, and of four plots of approximately 150 m^2 in the area surrounding the pond (hereafter termed sampling units). A preliminary evaluation of the spatial ecology of *M. colubrinus* suggested that the average movement between consecutive observations [distance between consecutive observations = 20 ± 22 m; time between observations= 25 ± 31 days (mean ± SD)] is below the size of our sampling units (F. Licata, unpublished data). We surveyed each sampling unit both during the early (from 29 January to 21 February 2019) and late (from 23 April to 18 May 2019) wet season, to account for variability in activity patterns of the species. Temperature and rainfall regimes changed considerably between the two periods. In April–May, temperatures were on average 2.3°C lower, while cumulative rainfall was nearly five times higher (4,106 mm vs. 822 mm in the period of January–February). During each period, we visited all sampling units 8 times, for a total of 16 visits over the early and late wet season. Surveys started at dusk, when this species is most active, and two experienced observers counted all active snakes (interval between visits 3.4 ± 1.9 days; sampling unit visit duration ~10 minutes).

We used *N*-mixture models, including an extension for open population (Dail and Madsen 2011), to estimate snake abundance from spatially and temporally repeated count data. *N*-mixture models jointly estimate the abundance and detection of animals on the basis of repeat surveys, without the need to capture and mark individuals (Royle 2004). Some studies highlight that obtaining joint estimates of detection probability and abundance can be problematic and *N*-mixture models are sensitive to violations of assumptions (Barker et al. 2018; Link et al. 2018; Duarte et al. 2018). Nonetheless, analyses of real-world data suggested that this approach provides reliable abundance estimates of wild animals (Kéry 2018; Ficetola et al. 2018a) in multiple ecological contexts (e.g., Romano et al. 2017; Costa et al. 2019).

To inform models, we considered three potential detection covariates: time of the survey, temperature at the time of the survey (°C), and total rainfall during the 24h before the survey (mm). Weather conditions were obtained from the local meteorological station, located at Toamasina airport (~7 km from the study site). Prior to analysis, detection covariates were scaled to allow comparison of the estimated effect sizes. Models were fitted using a Zero-Inflated Poisson error distribution (ZIP) rather than Poisson models, as the ZIP model showed a lower second order Akaike's information Criterion than the corresponding Poisson model (i.e., AIC_c) (Akaike 1973; Burnham and Anderson 2002). We did not consider Negative Binomial models because of their convergence issues (Kéry 2018). We chose to set the value of the upper limit of integration (K) to “100 + maximum observed species abundance”, as this value provides stable and robust abundance estimates (Ficetola et al. 2018b). We built models with all possible combinations of detection covariates, and retained the one with the lowest AIC_c value. The population was not closed between the two survey periods; we therefore tested against the default “constant” dynamic scenario, which implies no relationship between apparent survival and recruitment (Dail and Madsen 2011). We tested four possible population dynamics between the two seasons: a) no temporal trend; b) exponential trend; c) Ricker model; d) Gompertz trend (Hostetler and Chandler 2015), and retained the model with the lowest AIC_c (Burnham and Anderson 2002). We then used empirical Bayes methods to estimate the posterior distribution of snake abundances at the survey sites. We tested the global model for goodness-of-fit by means of a Pearson chi-square test, using a parametric bootstrap procedure (5,000 re-samplings) (MacKenzie and Bailey 2004), which showed that our data were not overdispersed and the model provides adequate fit to the data (c-hat 1.18; P 0.13). The model building procedure was conducted in R environment (version 3.6.1) (R Core Team 2020), using the package “unmarked” for modelling abundances (Fiske and

Chandler 2011) and “AICcmodavg” to compute the goodness-of-fit test (Mazerolle 2020) .

Monthly Mortality Rates in Madagascarophis colubrinus

We used the mortality events observed in the study area to obtain an estimate of monthly mortality rates of snakes due to toad poisoning. To provide a monthly figure of toad poisoning mortality rates we considered a subset (n = 7) of all dead snake observations (Supplementary Information 1 Table S1) collected in the sampling units where snake abundances were estimated between 23 December 2018 and 21 February 2019 and between 23 April to 18 May 2019. We excluded from the analysis of mortality rate those carcasses found outside of the study area where snake abundances were estimated and those for which residence time (i.e., the date of death) could not be established (Supplementary Information 1 Table S1). We averaged the number of dead snakes found over the duration of the survey period (n = 86 days). As decomposing carcasses gave off a strong smell facilitating their detection, and the interval between visits (median = 2 days; range = 1–12 days) was short enough to exclude total decomposition of the carcasses (Parmenter and MacMahon 2009), we infer that we documented most mortality events. Similarly, our observation of snake/toad interactions in Analabe suggest a prompt snake death after biting a toad (see also Results). Nevertheless, it is possible that some dead snakes remained undetected, thus our estimates represent a lower boundary of mortality rates.

Results

Radiotelemetry of Duttaphrynus melanostictus

Toads of both sexes and varying sizes inhabited the forest. The first toad observation within Analabe forest occurred on 23 November 2018, and a total of 18 toads (6 adult females, 2 males and 10 subadults) were observed during the entire survey period.

Adult individuals were found to be resident and showed limited vagility. Eight tagged adult toads were located 26 times (2–7 locations/toad) after their capture. Two toads lost their harnesses after 12 and 19 days of radio-tracking, respectively. All movements were recorded within Analabe forest or along its edges. Omitting observations of individuals that remained in the same shelter site on consecutive dates (2 of 26 cases), the mean distance between subsequent positions was 19 m (range= 1.4–55.7 m). The range span of toad locations was on average 28.4 m (range= 3.1–66 m), while the average Minimum Convex Polygon calculated for six individuals was 189.2 m^2 (range= 1–450 m^2). During the daytime, toads sheltered predominantly in leaf litter (16 of 23 cases), often partially or totally exposed, but were also found under rotten tree trunks, between roots, or inside cavities in the ground. In addition to the toads that lost their harnesses, two individuals died after predation during the tracking period. The first individual was found dead on 6 December 2018 after attempted predation by a cat-eyed snake, which was also found dead in close proximity (Supplementary Information 1 Table S1). The second toad was totally consumed by an unidentified predator (possibly a mammal, based on the marks on the remaining radio-tracking equipment left behind by the predator), and was found on 12 December 2018. The inspection of surrounding areas did not lead to the identification of any carcasses.

Abundances of Madagascarophis colubrinus

In our repeated surveys we counted fifty-four cat-eyed snakes (range 0–3 individuals per survey per sampling unit). Snakes were detected in all sampling units. The best AIC_c N-mixture model assumed no temporal trend in abundance and suggested that rainfall before the survey positively influenced the detection of snakes ($B = 0.455$, $p < 0.001$; Table 1). The estimated per-survey individual detection probability was 0.062 ± 0.058 (mean ± SE) and the estimated total abundance was 41 (95% CI = 31–53) and 44 (95% CI = 36–54) snakes for the first and second survey periods, respectively.

Mortality of Madagascarophis colubrinus

Although encountering carcasses of small vertebrates in rainforest habitat is generally a rare event (Rouquet et al. 2005), between 23 December 2018 and 21 February 2019 and between 23 April to 18 May 2019 we found nine cat-eyed snake carcasses in Analabe forest (Fig. 1c; Supplementary Information 1 Fig. S1, Table S1), plus three snake skeletons that could not be identified. All carcasses lacked any evident external injuries or trauma. In four cases, dead toads were found almost intact in the stomach, mouth, or next to the body of the snakes (Fig. 1c; Supplementary Information 1 Fig. S1, Table S1). In addition, the observation of an adult toad with a clear snakebite mark on the head (Supplementary Information 1 Fig. S1g), suggests that toads can sometimes survive snake predation attempts, despite likely poisoning the snake.

Considering an average population size of 43 (range = 33–54) snakes in the study area, and that we found approximately two poisoned snakes per month in the surveyed area, the resulting average monthly rate of mortality of this population was estimated to be at least 5.7% (range = 4.5–7.4; Fig. 1d).

Discussion

In this study we documented for the first time that the Asian common toad has successfully invaded forested habitats of Madagascar. However, the likelihood and magnitude of the effects of the invasion on rainforest communities will depend mostly on the suitability of forest habitat for toad reproduction, such as the availability of lentic water bodies. The eastern rainforest belt of Madagascar is dominated by the presence of steep slopes and by the occurrence of numerous brooks and rivers (Andreone and Luiselli 2000; Vences et al. 2002). Accordingly, the majority of Malagasy amphibians breed and metamorphose in running waters or phytotelmata (Vences et al. 2002; Glaw and Vences 2007; Strauß et al. 2010). The Asian common toad breeds in lentic waters, which are generally scarce in forested habitat. Topographic constraints in the forested slopes of eastern Madagascar could limit the spread of the toad invasion, and control strategies targeting suitable breeding sites for toads should be considered to limit the establishment of breeding populations in targeted areas.

The predicted vulnerability of Malagasy vertebrates to toad toxins raises major concerns about the cascading events that this invasion could trigger, although species-specific interactions remain difficult to quantify and predict (Marshall et al. 2018). Documenting the presence of the toad in a forested habitat and quantifying the lethal effects on an endemic snake allowed us to shed light on the possible interactions between an invasive toad and a native Malagasy predator, ultimately bringing into focus the management actions to be undertaken and the major risks associated with this invasion.

Likely Interactions with the Asian Common Toad

Amphibians are an abundant and diverse component of Malagasy rainforests, and several vertebrate species are known to prey on them (e.g., tenrecs [Olson 2013], plated lizards [Jovanovic et al. 2009], freshwater turtles [Luiselli et al. 2011], crocodiles [Wallace & Leslie 2008], carnivores [Farris et al. 2015]). Based on traits likely to affect how these native predators interact with the Asian common toad (e.g., feeding habits, foraging behavior and pattern of activity), nocturnal carnivores and snakes are the predators that will likely suffer most from the invader (Marshall 2018). Moreover, a tendency for crepuscular activity by the invasive toad increases the likelihood of interactions with diurnal native predators (F. Licata, pers. obs.).

Madagascar is a hotspot of snake diversity with 100 endemic species (Uetz et al. 2020), the vast majority of which originated from a single large radiation (Burbrink et al. 2019). Snake communities are mostly represented by small and medium-sized species which exhibit terrestrial or arboreal feeding habits and dietary preferences oriented towards lizards and frogs (Andreone and Luiselli 2000); none of them are predicted to have physiological resistance to toad toxins (Marshall et al. 2018). In addition to cat-eyed snakes, anurophagy has been reported in 11 other genera of Malagasy snakes: *Acrantophis* (Heying 2001), *Alluadina* (Hutter et al. 2018), *Compsophis* (Cadle 1996; Andreone and Luiselli 2000; Eudeline et al. 2015; Hutter et al. 2018), *Dromicodryas* (Andreone and Luiselli 2000; Gandola, et al. 2013), *Ithycyphus* (Glaw and Vences 2007), *Leioheterodon* (Rosa et al. 2010), *Liopholidophis* (Glaw et al. 2007), *Mimophis* (Glaw and Vences 2007), *Pseudoxyrhopus* (Andreone and Luiselli 2000), *Sanzinia* (Raxworthy 2003; Glaw and Vences 2007) and *Thamnosophis* (Glaw and Vences 2007; Jovanovic et al. 2009; Eudeline et al. 2015). Yet, dietary preferences of many species are largely unknown. The impact of toad poisoning on each species will depend on multiple factors (e.g., habitat and predator body size; Feit & Letnic 2015) but, among frog-eating snakes, diurnal (e.g., *Dromicodryas*, *Leioheterodon*, *Mimophis*, *Liopholidophis*, and *Thamnosophis*) or arboreal species (e.g., some *Compsophis* spp. and *Ithycyphus* spp.) are expected to have less interactions with the invasive toad.

Assessing the Effects of the Invasion

A monthly mortality of 5.7% can potentially cause a decline of approximately 11% of the population from the first to the second study period. Such a decline was not detected in our second sampling period due to the low detection probability estimated for this population (per-individual detection probability = 0.062 ± 0.05), the short temporal interval between the two sampling periods, and the limited number of sampling sites, as demonstrated in simulation studies (Ficetola et al. 2018b). Despite the apparently territorial nature of *M. colubrinus* (see Material and Methods), a lack of geographic closure of our sampling units between survey periods could have hindered precise estimates of abundance, overestimating monthly mortality rates. A long-term study in multiple invaded/un-invaded localities, with individual identification of snakes (e.g., capture-mark-recapture; Lindberg 2012), will clarify the predator population trends and help obtain a more robust estimate of the toad poisoning effects. If the rate of mortality is similar to our estimates, and it is constant through the year, then annual mortality might be higher than 50% in the studied snake population, a level likely to cause extirpation. These figures are nearly double the measured mortality rates of snakes caused by cane toads in Australia (e.g., Phillips et al. 2010). This difference could be due to multiple context-dependent factors, such as the increased activity of cat-eyed snakes during the survey period (i.e., the wet season), which translates into higher probability of interaction with the toxic prey. In addition, habitat suitability for the invasive species (Jolly et al. 2015), and community structure (Radford and Fairman 2015), might also play a key role in determining the impact of toad poisoning (Doody et al. 2009, 2013; Kraus 2015).

Gathering abundance data of target species that exploit habitats at risk of invasion is crucial to assess the long-term effects of toad impact on native communities. However, quantitative information on the abundance of native vertebrates is extremely limited in Madagascar, especially for snakes, which generally have a low detection probability and are difficult to encounter in the field (Durso et al. 2011). The most widespread and easily detectable Malagasy species, which can potentially suffer from toad poisoning, can serve as ecological indicators of toad impact on native communities, and study of their abundances before and after toad arrival could enable a standardized assessment of the effects of the invasion (see Supplementary Information 1).

Toad-induced decline of snakes in Madagascar can reduce predation pressure on rodents and insectivores and facilitate their expansion, especially if these species are not impacted by toad poisoning, such as the rat *Rattus norvegicus* (Marshall et al. 2018). An increase of rats may result in reduced harvest yields and stored food quality (e.g., Duplantier and Rakotondravony 1999), and potentially increase the transmission rates of rodent-borne zoonotic diseases (Han et al. 2016). We expect cat-eyed snake populations across rural and suburban areas of Toamasina to be severely affected by the toad invasion. Future research should be directed toward understanding indirect facilitation of human-commensal, disease-bearing rodents after predator removal, and potential relevance to human health. If confirmed, we suggest that the buffering role of snakes should be included under the umbrella of the One Health approach aiming at addressing good health and well-being issues in Madagascar.

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Figures

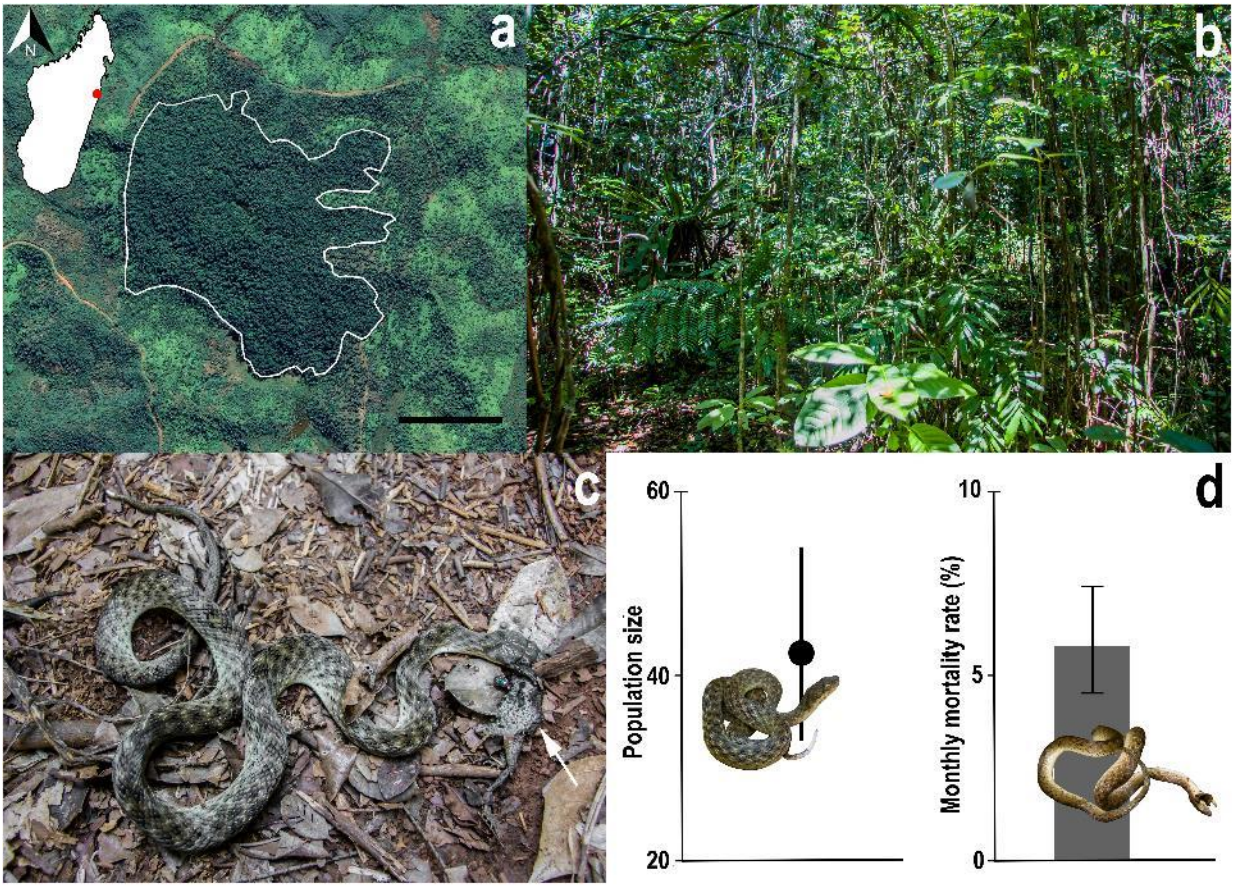

Fig. 1. Toad poisoning effect on *Madagascarophis colubrinus*: a) Analabe forest (scale bar = 200 m) (Map data: Google, Maxar Technologies); b) habitat in Analabe forest; c) carcass of *M. colubrinus* lethally poisoned by a subadult *Duttaphrynus melanostictus* (arrow); d) estimated average snake population size (left) and monthly mortality rate for toad poisoning in *M. colubrinus* (right), with bars indicating 95% confidence interval.

Table 1. Model selection based on Akaike's Information Criterion corrected for small samples (AIC_c), number of parameters (nPars), the difference AIC_c from the best fit models (ΔAIC_c), and model weights ($AIC_c wt$).

	nPars	**AIC_c**	**ΔAIC_c**	**$AIC_c wt$**
A) Initial abundance				
ZIP λ(.)γ(.)ω(.)[Constant]p(.)	5	231.03	0.00	0.77
Poisson λ(.)γ(.)ω(.)[Constant]p(.)	4	233.47	2.44	0.23
B) Detection				
λ(.)γ(.)ω(.)[Constant]p(Rain)	6	217.15	0.00	0.99
λ(.)γ(.)ω(.)[Constant]p(.)	5	231.03	13.88	<0.01
C) Dynamics				
λ(.)γ(.)ω(.)[No Trend]p(Rain)	5	215.56	0.00	0.43
λ(.)γ(.)ω(.)[Exponential]p(Rain)	5	216.92	1.37	0.22
λ(.)γ(.)ω(.)[Constant]p(Rain)	6	217.15	1.59	0.19
λ(.)γ(.)ω(.)[Ricker]p(Rain)	6	218.95	3.39	0.08
λ(.)γ(.)ω(.)[Gompertz]p(Rain)	6	218.95	3.39	0.08