Small population size and possible extirpation of the threatened Malagasy poison frog *Mantella cowanii*

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Abstract

Amphibians are experiencing severe population declines, requiring targeted conservation action for the most threatened species and habitats. Unfortunately, we do not know the basic demographic traits of most species, which hinders population recovery efforts. We studied one of Madagascar's most threatened frog species, the harlequin mantella (*Mantella cowanii*), to confirm it is still present at historic localities and estimate annual survival and population sizes. We surveyed eleven of all thirteen known localities and were able to detect the species at eight. Using a naïve estimate of detection probability from sites with confirmed presence, we estimated 1.54 surveys (95% CI: 1.10–2.37) are needed to infer absence with 95% confidence, suggesting the three populations where we did not detect *M. cowanii* are now extirpated. However, we also discovered two new populations. Repeated annual surveys at three sites showed population sizes ranged from 13–137 adults over 3–8 years, with the most intensively surveyed site experiencing a >80% reduction in population size during 2015–2023. Annual adult survival was moderately high (0.529–0.618) and we recaptured five individuals in 2022 and one in 2023 first captured as adults in 2015, revealing the maximum lifespan of the species in nature can reach nine years and beyond. Our results show *M. cowanii* is characterized by a slower life history pace than other *Mantella* species, putting it at greater extinction risk. Illegal collection for the international pet trade and continued habitat degradation are the main threats to the species. We recommend conservation efforts continue monitoring populations and reassess the IUCN Red List status because it may be Critically Endangered rather than Endangered based on population size and trends.

Introduction

Amphibian species are facing extinction rates at least 22 times faster than the average rate during the 10 millennia before industrialization, resulting in their status as the most threatened vertebrate class (Ceballos et al., 2015; Luedtke et al., 2023). Many species are experiencing severe population declines, leading to widespread range contractions through extirpation (e.g., Beyer and Manica 2020; Granados-Martínez et al. 2021; Patla and Peterson 2022). Habitat loss is the largest threat to amphibians, but infectious diseases, invasive species, climate change, overexploitation, and pollution are all responsible for declines and interact in complex ways (Collins, 2010; Grant, Miller & Muths, 2020). Such threats and population trends highlight the immediate need for increased conservation, especially targeted toward the most threatened species and their habitats.

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The island of Madagascar supports extraordinary amphibian species richness and endemism, with more than 415 described endemic frog species representing five anuran clades of independent origin (Crottini et al., 2012; Antonelli et al., 2022; AmphibiaWeb 2023). Alarmingly, 46.4% of assessed Malagasy frog species are threatened, owing largely to deforestation (Ralimanana et al., 2022; IUCN, 2023). Deforestation has eliminated as much as a quarter of the tree cover on the island over the last 25 years and the rate has only increased since 2005 (Vieilledent et al., 2018; Suzzi-Simmons, 2023). Consequently, many frog species in Madagascar have patchy distributions restricted to isolated pockets of forest in an otherwise inhospitable landscape (Lehtinen & Ramanamanjato, 2006). So far, there have been no documented modern frog species extinctions in Madagascar (Andreone et al., 2008, 2021), but many records of species presence are from biological inventories conducted decades ago in areas with high rates of land use change. Verifying species presence and confirming the extant distribution of threatened species is some of the most vital information for informing conservation (Villero et al., 2017). Relatedly, we know little about frog population trends in Madagascar, even for highly threatened species. The lack of demographic information is not unique to Madagascar; we do not know survival or fertility rates for 87.5% of amphibian species globally (Conde et al., 2019). Baseline estimates of survival, recruitment, and other demographic traits are urgently needed to improve conservation efforts and inform management decisions (Grant, Miller & Muths, 2020).

Some of the most well-known amphibians in Madagascar are the Malagasy poison frogs in the genus *Mantella*. One species (*M. laevigata*) exhibits parental care and all members of this genus display aposematic coloration to warn predators of their poisonous skin alkaloids sequestered from prey (Vences et al., 2022). As such, they are familiar examples of convergent evolution with Neotropical dendrobatids (Daly, Highet & Myers, 1984; Chiari et al., 2004; Fischer et al., 2019). While several *Mantella* species are widespread and have been found in degraded habitat and agricultural plantations (e.g., *M. betsileo*, *M. ebenaui*, and *M. viridis*, Vences et al., 1999; Andreone et al., 2006; Crottini et al., 2012), most are restricted to small areas, have highly localized populations, show a recent dramatic demographic decline, and are threatened by ongoing habitat degradation (e.g., Crottini et al. 2019). Compounding the threat of habitat loss is overexploitation; thousands of wild poison frogs are exported annually from Madagascar for the international pet trade (Rabemananjara et al., 2007b), though export quotas have been restricted recently to smaller quantities of just six species (CITES, 2022).

The harlequin mantella frog (*M. cowanii*) is one of the most threatened *Mantella* species, with a small and fragmented distribution in the central highlands. This region of Madagascar was formerly a mosaic of grassland, woodland, and subhumid forest,

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covering the mountainous area between the island's humid east and dryer west (Yoder et al., 2016). Today the central highlands consist mostly of secondary grasses and land converted for subsistence agriculture and cattle grazing, with little humid forest remaining (Andriambeloson et al., 2021; Ranarilalatiana et al., 2022). Thirteen localities of *M. cowanii* are known from the region: six in a cluster around the town of Antoetra, five 80 km northwest on the Itremo Massif, and two isolated localities located >100 km north of all other known populations, one near Betafo and the other east of Antakasina (Rabibisoa, 2008; Rabibisoa et al., 2009). All populations occur along mountainous streams with large boulders and adjacent wet rockfaces. While some sites still have intact gallery forests, others are almost entirely devoid of trees (Fig. 1). Additionally, due to its striking black and orange coloration (Fig. 2), *M. cowanii* was heavily exploited for the international pet trade during the 1990s and early 2000s (Andreone, Mercurio & Mattioli, 2006). From 1994–2003, several thousand frogs recorded as *M. cowanii* were exported from Madagascar for commercial purposes, after which legal trade was halted, and the export quota was set to zero (Rabemananjara et al., 2007b; CITES, 2022).

Despite heavy collection pressure and ongoing habitat loss, the demographic characteristics of the remaining *M. cowanii* populations have not been studied. Additionally, some populations are known from only one or two scientific expeditions carried out decades ago and could already be extirpated. In 2021 the *Mantella cowanii* Action Plan (McAP) was launched to draw attention to the species and develop a blueprint for its conservation (Andreone et al., 2020; Rakotoarison, Ndriantsoa & Rabemananjara, 2022). The McAP builds on the initial conservation strategy by Rabibisoa (2008). We aimed to fill critical research needs in the McAP by 1) confirming the presence of *M. cowanii* at localities across its range and 2) if present, estimating the key demographic traits of survival and population size.

Materials & Methods

Study Sites

We surveyed 11 of 13 known *M. cowanii* localities, nine in the Amoron'i Mania Region and two in the Vakinankaratra Region (Fig. 3). Sites ranged in elevation ~1380–2120 m asl. We repeatedly surveyed three sites (Ambatofotsy, Soamasaka, and Fohisokina) over 3–8 years for 2–20 days/year to estimate demographic traits (Table 1). The remaining eight sites (Ambinanitelo, Andraholoma, Antakasina, Antsirakambiaty, Bekaraka, Farihimazava, Tsimabeomby, and Vatolampy) were visited up to two times for 1–6 days to confirm species presence. Only two sites have some form of habitat protection: Fohisokina (also known as Vohisokina) is community-managed with an NGO (Nowakowski & Angulo, 2015), and Antsirakambiaty falls within the boundaries of Itremo Massif Protected Area (Alvarado, Silva & Archibald, 2018). The other sites are unmanaged and without legal protection.

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Data Collection

Fieldwork was conducted during the onset of the rainy season from late November to mid-January when *M. cowanii* is active and detectable. Surveys were carried out in the morning during 5–8h, but at Fohisokina in 2015, we also surveyed just before dusk during 16–18h. We searched for frogs visually, walking together in teams of 2–7 people along the stream or adjacent wet rockface. If we heard a frog calling, we used the call to help find its location. Stream segment length varied from 38 m at Bekaraka to 690 m at Ambatofotsy. At Fohsiokina, we surveyed along six 50 m-long transects rather than opportunistically throughout the entire site to accomplish additional research objectives (see Newton-Youens 2017).

After capturing a frog, we held it in a plastic bag (or a petri dish in 2015 at Fohisokina), marking the location with a GPS point, flagging tape, and a unique number. We measured snout-to-vent length with digital calipers or a ruler. Individuals <22 mm were recorded as subadults under one-year post-metamorphosis based on Guarino et al. 2008. Weight was recorded with a digital scale to the nearest 0.01 g, and sex was recorded based on whether an individual had been calling before capture and, if not, body size (Tessa et al. 2009). We also took dorsal and ventral photographs, allowing us to identify recaptured individuals because each frog has a unique ventral pattern (Fig. 4). Such photographic capture-mark-recapture techniques can be more accurate and are less invasive than traditional toe-clipping or visual implant elastomers (Caorsi, Santos, and Grant 2012; Davis, VanCompernolle, and Dickens 2020). Initially, we tried using photographic matching software to automate identifying individuals (sensu Edmonds et al. 2019), but photograph angle and quality varied between days, sites, and years, so the process was prone to false negatives. Instead, one of us (D. Edmonds) visually examined all ventral photographs side-by-side and recorded when there was a match. Following photographs and measurements, frogs were released in the location where they were captured.

We followed all applicable international, national, and institutional guidelines for the care and use of animals. The study methods were approved by the Ministère de l'Environnement et du Développement Durable in permits N°173/20/MEDD/SG/DGGGE/DAPRNE/SCBE.Re, N°439/21/MEDD/SG/DGGGE/DAPRNE/SCBE.Re, and N°173/22/MEDD/SG/DGGGE/DAPRNE/SCBE.Re and by the University of Illinois Urbana-Champaign Institutional Animal Care and Use Committee in protocol #21180.

Analysis

We used a robust design capture-mark-recapture model to estimate population size (N) and apparent annual survival (φ) at Ambatofotsy, Fohisokina, and Soamasaka. These sites were selected because we had sampled them for at least three years, the

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minimum required for estimating annual survival. Our analysis compared 17 models, all incorporating site as a group-level effect. We considered models with either constant or site-specific φ and the temporary emigration parameters γ'' and γ' either constrained to 0 assuming no movement or set equal assuming random emigration. To account for individual heterogeneity in capture probability (p), we included a random effect of individual on p. Additionally, we compared models with capture probability covariates of site, year, number of surveyors, and survey effort calculated as the number of surveyors multiplied by the survey duration in minutes. We could not include environmental covariates that might be associated with capture probability because they were not collected consistently across all sites and years. To compare candidate models, we ranked them using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). Models with $\Delta AIC_c < 2$ were considered to have support. We analyzed capture-mark-recapture data in program MARK through the *RMark* interface (White & Burnham, 1999; Laake, 2013) and assessed the goodness-of-fit with package *R2ucare* in R version 4.2.0 (Gimenez et al., 2018; R Core Team, 2022).

To infer absence if we did not detect *M. cowanii* at a historic locality, we estimated detection probability with a single-season occupancy model in package *unmarked* (Fiske and Chandler 2011). Data from nine localities with confirmed presence and at least three surveys were used to generate a naïve estimate of detection probability assuming constant detection and occupancy. We then followed Pellet and Schmidt (2005) to estimate the number of surveys needed to detect the species as:

$$N_{min} = \frac{\ln(0.05)}{\ln(1-p)}$$

where N_{min} is the minimum number of surveys, p is the detection probability, and 0.05 is the confidence level needed to be 95% certain of absence, assuming independent and comparable surveys. Using the number of surveys, we then calculated the confidence level around an observed absence given N number of surveys as:

$$conf = e^{N*\ln(p)}$$

Results

Verifying Species Presence

We confirmed *M. cowanii* presence at 8 of 11 surveyed localities and identified 2 previously unrecorded populations. However, we failed to detect the species at the historical localities of Andraholoma, Tsimabeomby, and Vatolampy. The naïve detection probability from sites with confirmed presence was 0.86 (95% CI: 0.72–0.93), showing it takes 1.54 surveys (95% CI: 1.10–2.37) to be 95% confident a population is extirpated and 2.37 surveys (95% CI: 1.69–3.65) to be 99% confident. With at least two days of

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surveys at Andraholoma and Vatolampy, we can be >97.9% (95% CI: 91.9–99.9%) confident the populations are extirpated and 85.7% (95% CI: 71.7–93.4%) confident there are no *M. cowanii* at Tsimabeomby.

Capture Patterns Across Sites

We made 764 captures of 280 individuals across all study sites and years, excluding putative *M. baroni* x *M. cowanii* hybrids. All but 8 frogs were adults. Over half of all captures were at Fohisokina, where we caught 149 individuals 481 times. Six individuals at Fohisokina were recaptured 7 years after initially being caught in 2015 as adults (Fig. 4), one of which was recaptured again in year 8 in 2023. At our second most intensively surveyed site, Soamasaka, we made 137 captures of 40 individuals during annual fieldwork in 2020–2023. Three frogs were recaptured 4 years after their initial encounter in 2020, and 4 were recaptured 3 years apart. At Ambatofotsy, we conducted surveys in 2021, 2022, and 2023 and made 76 captures of 32 individuals, all adults.

Annual Survival and Population Sizes

The most parsimonious capture-mark-recapture model had capture probability p and annual adult survival φ varying by site (Table 2). Models with no movement generally performed better than those with random emigration (Table 2). The top model estimated population sizes (N) ranging from 13–137 adult frogs per site across years (Fig 5). The highest N estimate was from Fohisokina in 2015 (137, 95% CI: 120–170) and the lowest from Soamasaka in 2023 (13, 95% CI: 11–22). Fohisokina showed a decreasing population size during 2015–2023, whereas Soamasaka and Ambatofotsy were relatively stable over a shorter period (Fig. 5). There was strong support for site-varying survival (Table 2), with the estimated annual adult survival more precise for Fohisokina than Soamasaka due to the longer study duration (Fig. 6). For Ambatofotsy, the survival estimate was too imprecise to be informative because the data spanned only three years and only a small number of frogs were captured each year. Overall, the annual survival estimates at Fohisokina and Soamasaka were comparable, although the estimate from Soamasaka was lower than Fohisokina (Fig. 6).

Discussion

Our results demonstrate *M. cowanii* was still present at no less than ten localities in 2022–2023, but the population size is very small for at least three sites (<50 adults per site). Extrapolating across all known localities, in the worst-case scenario, the total adult population size for the species may number <500 individuals. However, frog populations naturally fluctuate in abundance, and a snapshot over several years can easily lead to erroneous conclusions that populations are declining when they are stable (Pechmann et al., 1991; Blaustein, Wake & Sousa, 1994; Meyer, Schmidt &

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Grossenbacher, 1998). Such fluctuations are typical of species with fast life histories, where fecundity is high and generation time short, thus, demographic rates tend to vary (Sæther et al., 2004, 2013). Additionally, amphibian populations fluctuate more for pond breeding species and less for terrestrial and stream breeding species (Green, 2003). Considering *M. cowanii* is a terrestrial stream-breeding frog with comparatively low reproductive output (20–57 eggs per egg mass; Tessa et al. 2009), relatively high annual adult survival, and a maximum lifespan in nature of at least nine years, we believe our results are not an artifact of stochastic fluctuations in population size.

We highlight three possible factors contributing to the >80% population decline at Fohisokina between 2015 and 2023. First, fires burnt much of Fohisokina in November 2020 at the start of their breeding season, just before our survey. Though *M. cowanii* presumably is protected from fire while sheltering in moist rock crevices and caves for much of the year, fire can cause mortality in terrestrial frogs when they are active above ground during the breeding season (e.g., Humphries and Sisson 2012; Potvin et al. 2017). Second, according to a European private breeder, in 2017 more than 100 *M. cowanii* were illicitly offered for sale in Germany, and an unknown number were offered again in 2021. As Fohisokina is the most easily accessed *M. cowanii* locality and was historically a collection site for the pet trade (Rabemananjara et al., 2007b), the frogs were possibly poached from Fohisokina. Lastly, although no records of chytridiomycosis have been confirmed in Madagascar and all frogs we sampled appeared healthy, the amphibian chytrid fungus *Batrachochytrium dendrobatidis* has been reported from the island, and in 2014 was detected on a single *M. cowanii* individual at Soamasaka ~5 km south of Fohisokina (Bletz et al., 2015). Therefore, we cannot rule out disease either.

At Vatolampy, we did not detect *M. cowanii* after six days of surveys and suspect the population is extirpated. Until our work, the site had not been surveyed since 2003–2004, when Andreone et al. (2007) and Rabemananjara et al. (2007a) collected tissue samples and voucher specimens from the population. Similarly, Andraholoma had not been surveyed since 2009 when the site was visited by one of us (C. Randrianantoandro) for one day and 5 individuals observed. Conversely, we question whether Tsimabeomby, the third site where we did not detect *M. cowanii*, ever supported a population. We believe the locality was possibly published in error by Rabibisoa (2008) because Tsimabeomby consists of a wet meadow, is without rocks or running water, is isolated from the next nearest population by >3 km, and the local people we worked with had never encountered *M. cowanii* there whereas they knew of the other populations. Nonetheless, *M. cowanii* could have been present but undetected during our surveys if the detection probability at Andraholoma, Tsimabeomby, and Vatolampy was lower than elsewhere. Additionally, the naïve estimate of detection probability we used to infer absence did not account for observer, environmental, or temporal factors influencing detection. Still, our team detected *M. cowanii* at other sites on the days we

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surveyed Andraholoma, Tsimabeomby, and Vatolampy, illustrating local environmental conditions were favorable for detecting *Mantella*. Re-surveying the three sites in the coming years will confirm if the populations are extirpated.

Some amphibian species are capable of dispersing long distances to recolonize suitable habitat (Marsh and Trenham 2001; Fonte, Mayer, and Lötters 2019), but we do not expect so for *M. cowanii* in Madagascar's degraded highland landscape. There are no studies on the movement of Madagascar's poison frogs (but see Andreone et al. 2013), however research on their Neotropical dendrobatid counterparts shows adults rarely move more than a few hundred meters from established territories (e.g., Ringler et al. 2009, Pašukonis et al. 2013; Beck et al. 2017; Pašukonis et al. 2019). Moreover, in a review of the dispersal ability of amphibians, Smith and Green (2005) found nearly half of studied species moved <400m. Historically, adult frogs may have moved between patches when there was more forest in the highlands. However, we suspect *Mantella* usually passively disperse when tadpoles are flushed between habitat patches during heavy rain. As such, natural recolonization of Vatolampy or Andraholoma is unlikely, especially considering the physiological, movement, and site fidelity constraints amphibians face (Blaustein, Wake & Sousa, 1994). At Vatolampy, the next closest locality is Farihimazava, 1.5 km northeast in a different valley, which supports mostly *M. baroni* and *M. baroni* x *M. cowanii* hybrids (Chiari et al., 2005; Andreone et al. 2007). For Andraholoma, the next closest locality is Andaobatofotsivava >7 km north, though admittedly, the area of the Itremo Massif is poorly explored and there could be additional unrecorded populations between the two. Indeed, we located two new localities during fieldwork.

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Previous skeletochronology research estimated the maximum lifespan of *M. cowanii* at three years (Guarino et al., 2008; Andreone et al., 2011), but we identified individuals at least eight years post-metamorphosis and one individual nine years. Skeletochronology is known to underestimate the ages of older individuals because skeletal growth rings progressively converge with age, and amphibian bone tissue is prone to reabsorption (Eden et al., 2007; Sinsch, 2015). Our results show the advantages of using capture-mark-recapture surveys for estimating demographic traits if resources are available. The long lifespan of *M. cowanii* is notable when considered together with their reproductive output and body size. The species is one of the largest in the genus, has the largest egg diameter, and has the lowest number of eggs per mass, exemplifying their slow life history compared to other *Mantella* species (Tessa et al. 2009). All of this aligns with our discovery that *M. cowanii* has the longest lifespan for the genus. Life history traits often follow altitudinal clines, with slower traits associated with higher altitudes (Hille & Cooper, 2015; Laiolo & Obeso, 2017). Indeed, amphibians tend to live longer and have larger body sizes at higher altitudes (Morrison & Hero, 2003; Andreone et al. 2004); *M. cowanii* is no exception (Tessa et al. 2009). Such

patterns also occur within species across altitudinal gradients (Zhang & Lu, 2012). Considering the *M. cowanii* from Betafo populations occur ~500m higher than where we recorded ~8–9-year-old individuals, frogs from Betafo may live even longer. Such slow life history traits also have conservation implications because they are associated with higher extinction risk (Webb, Brook & Shine, 2002). Given the relatively long lifespan and low reproductive output of *M. cowanii*, the success of recovery efforts for the species may not be as rapid as in other related amphibian species.

To ensure populations remain extant, we must better identify the causes of declines and the magnitude of threats. Screening populations for *Bd* and monitoring for illicit *M. cowanii* in the pet trade are obvious actions, but disentangling the threat of habitat loss is more complicated. The number of trees remaining at sites varies from intact closed-canopy forest to rocky landscapes almost entirely devoid of trees, so the degree to which deforestation is a threat may depend on additional habitat characteristics. Newton-Youens (2017) identified rock caves and refuges as essential habitat features, and speculated they might be used for breeding, though so far, no eggs, tadpoles, or newly metamorphosed individuals have been found in nature. Studies on the microhabitat preferences and activity levels of *M. cowanii*, like those carried out by Edwards et al. (2019, 2022) for *M. aurantiaca*, would further help identify the most critical habitat features to protect and the best time to survey sites. Likewise, better information about habitat requirements could be used to locate new sites with unprotected populations we do not know about. All known *M. cowanii* populations are centered around four isolated sites with likely past connectivity when the highlands were an intact forest-grassland mosaic (Bond, Silander & Ratsirarson, 2023). Fieldwork in the remote areas between the four population centers could uncover additional isolated *M. cowanii* populations, but time is running out.

Conclusions

We set out to verify the presence and estimate key demographic traits for one of Madagascar's most threatened frog species and found several historical localities are likely extirpated while others are extremely small. Unfortunately, our results are not unique to Madagascar but represent a global trend in amphibian populations (Stuart et al., 2004; Grant et al., 2016). Amphibians are at the forefront of the extinction crisis, and population monitoring is essential to measure responses to conservation actions and detect declines before recovery is impossible. We used capture-mark-recapture methods to estimate abundance at three localities (Ambatofotsy, Soamasaka, and Fohisokina; Fig. 3), but less costly approaches relying on presence-absence data are likely suitable for monitoring *M. cowanii* across its entire range (Joseph et al., 2006; Jones, 2011). When enacted with local people as part of a broader program, monitoring can galvanize conservation efforts by adding value to a threatened species and instilling pride in local communities (Andrianandrasana et al., 2005; Danielsen, Burgess &

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Balmford, 2005). As we have shown, the causes of declines are often unclear without adequate information on a species' basic ecology and life history. For *M. cowanii*, we recommend further research run concurrently with conservation efforts and focus on determining the relative impact of disease, illegal trade, and habitat loss. We also recommend reassessing the IUCN Red List status of *M. cowanii*. The species was last assessed in 2014 as Endangered but it may qualify for the Critically Endangered status based on our estimates of population sizes and trends.

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