



Integrating dynamic occupancy modeling and genetics to infer the status of the imperiled flattened musk turtle



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ABSTRACT

Understanding changes in biodiversity at the levels of species and genes is imperative for effective conservation management. Here, we present a study that uses both dynamic occupancy modeling and mtDNA genetic analyses to quantify hypothesized population extinction and genetic introgression in the morphologically unique and federally threatened flattened musk turtle, *Sternotherus depressus*, endemic to rocky creeks in north-central Alabama, USA. Incorporating historic surveys in dynamic occupancy modeling shows that the flattened musk turtle has been extirpated from 32–56% of its historically occupied distribution. We find strong support for unidirectional mtDNA introgression from a closely related species into the flattened musk turtle. Additionally flattened musk turtles with allospecific mtDNA have an intermediate morphology (level of carapace depression) when compared to pure forms suggesting overall genomic hybridization that may have negative fitness effects for the species. Overall, this research provides a necessary quantitative evaluation of both local extinction and hybridization in the flattened musk turtle and shows that both demographics and genetics are essential for effective management of the species.

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1. Introduction

Quantifying changes in fundamental measures of biodiversity (McNeely et al., 1990; Noss, 1990; Moritz, 2002; Rands et al., 2010) is a necessary first step in ensuring that conservation, management, and recovery actions of threatened species are adequate. Accurately inferring changes in a species' range, density, or demography through time is reliant upon monitoring natural populations (Yoccoz et al., 2001; Martin et al., 2007) whose distributions may be disjunct and vary in terms of the intensity of anthropogenic perturbations (Magurran et al., 2010). Many rare, imperiled, or cryptic species can be difficult to detect, even if present, which can make it even more challenging to assess species' status (Webb et al., 2014). Not accounting for major sources of error in sampling methodology (i.e. inaccurate detection, variation in detection, and surveyor error), can result in efforts that imprecisely or incorrectly reflect the status of an organism or ecosystem. Additionally, population level genetic diversity (McNeely et al., 1990; Reed and Frankham, 2003) and hybridization (Allendorf et al., 2001) should not be ignored in biological monitoring efforts. When designed well, studies aimed at monitoring natural populations should deliver information on demographic changes, identify possibly

irreversible population trends, and highlight ways to make conservation management more effective (Lindenmayer et al., 2012).

Because biological monitoring is reliant on actual surveys for individuals, or signs of individuals, such as feces, vocalizations, or environmental DNA (Thomsen and Willerslev, 2015), imperfect or variable detection of organisms can greatly bias or misinform data on species' population demographics (Yoccoz et al., 2001; Kéry, 2011). Recently, the application of occupancy modeling (MacKenzie et al., 2002; Tyre et al., 2003), which allows for imperfect and variable site detection of individuals to be included in monitoring, has greatly improved the power to accurately estimate the probability of site occupancy for species. Additionally, dynamic (or multi-season) occupancy modeling (MacKenzie et al., 2003), allows for the incorporation of imperfect and variable detection of individuals at particular sites or populations in multi-year studies. Through modeling season-specific occupancy under a Markovian process, whereby probability of site occupancy at any given time is reliant upon the probability of occupancy during the previous season, site specific probabilities of colonization or extinction can be estimated (MacKenzie et al., 2003; Kéry et al., 2013). Thus, dynamic occupancy modeling (DOM) has the distinct advantage of allowing for robust estimation of population extinction for species while accounting for factors that may cause imperfect or variable detection across their range (Kéry et al., 2013), which may be especially important for cryptic and rare species.

Although long term studies monitoring changes in species distributions and densities are often a first step in providing baselines for conservation biology (Yoccoz et al., 2001; Clutton-Brock and Sheldon,

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2010), such studies are limited in their ability to detect proximate causes of declining population size (Clutton-Brock and Sheldon, 2010; Pagel and Schurr, 2012). Ultimately, many factors can influence survivorship at different life history stages (Coulson et al., 2001; Cahill et al., 2012), and species population declines can rarely be attributed to a single source (Brook et al., 2008). Recently, interest in the many genetic reasons (especially combined with other proximate causes) for population decline or extinction, including drift, habitat fragmentation, allelic loss, inability to remove deleterious mutations, inbreeding depression, and hybridization has become a major part of conservation biology (Frankham, 1995, 2005; Allendorf et al., 2013; Whiteley et al., 2015).

The recognition that many species may be experiencing genomic pollution or extinction due to hybridization and/or introgression (Rhymer and Simberloff, 1996; Allendorf et al., 2001), especially when mediated through human-induced pathways (Crispo et al., 2011), has made detection and quantification of hybridization an important new facet in conservation biology (Allendorf et al., 2001).

Hybridization and introgression can be difficult to detect without genetic data, but the effects are often negative and necessitate unique conservation management actions (Allendorf et al., 2001). For example, in the well-known case of hybridization between *Salvelinus confluentus* (bull trout) and introduced *Salvelinus fontinalis* (brook trout), hybrids rarely go beyond the F1 generation, thus hybridization results in wasted reproductive effort for the threatened bull trout which without hybridization would go towards propagating the species (Leary et al., 1993). Similarly, outbreeding depression, where hybrid or introgressed offspring have lower fitness than one or both parental forms, could result in population decline or extinction (Edmands, 2007).

On the opposite end of the spectrum, hybridization can result in complete genomic introgression and genetic assimilation — leading to the genomic extinction of a population or species. For example, anthropogenically mediated gene flow between *Argyranthemum* plants, occurring after roads were built over regions of uninhabitable lava beds in the Canary Islands, facilitated the genomic extirpation of some populations of the rare plant *Argyranthemum coronopifolium* with pure populations being replaced by hybrid swarms (Levin et al., 1996). Additionally, in New Zealand, similar genetic extinction occurred to native gray ducks following introduction of mallards to the islands (Gillespie, 1985; Rhymer and Simberloff, 1996). Individuals of hybrid ancestry can also have major ecological consequences; for example, hybrid tiger salamanders (*Ambystoma mavortium* x *californienses*) are able to outcompete native salamanders due to hybrid vigor (Fitzpatrick and Shaffer, 2004) and negatively impact other native wildlife through competition and/or expanded resource use (Ryan et al., 2009) as transgressive hybrids (extreme phenotypes in hybrids relative to either parental form; Rieseberg et al., 1999; Mallet, 2007; Dittrich-Reed and Fitzpatrick, 2013). Hybrid populations may even invade new habitats adding competitive pressure on native organisms or perform superiorly in intermediate or disturbed habitat, further fractioning native populations (Arnold and Hodges, 1995). Whether hybrids have reduced or increased fitness when compared to natural populations, understanding the causes of (especially if anthropogenically mediated; Crispo et al., 2011), extent of, and ecological impact of hybridization is integral to informing conservation decisions.

1.1. Study species

One such threatened species that is believed to have experienced major population reductions or extirpations (Mount, 1981; Ernst et al., 1983; Dodd, 1988; Fonnesebeck and Dodd, 2003) and hybridization with a closely related species (Estridge, 1970; Iverson, 1977) is the freshwater turtle — *Sternotherus depressus* (flattened musk turtle). The flattened musk turtle (FMT) was formally described by Tinkle and Webb (1955), and the species is known to inhabit only permanent streams of the Black Warrior River system north of the Fall Line

(Fig. 1; Iverson, 1977; Mount, 1981) in north central Alabama — an area approximately 12,528 km² (Buhlmann et al., 2009) containing about 670 linear miles of stream and river (Mount, 1981). Following survey work on the status of the turtle (reviewed in Mount, 1981; Ernst et al., 1983; Dodd et al., 1986), the species was listed as threatened under the Endangered Species Act of 1973 (U. S. Fish and Wildlife Service, 1987) and is currently considered Critically Endangered by the IUCN Red List (van Dijk, 2013). Both Mount (1981) and Ernst et al. (1983) performed comprehensive range wide surveys, providing baseline distribution and abundance data. Both authors described that the FMT was absent from or very rare in both historically occupied and/or suitable habitat, citing possible siltation and pollution from mining and agriculture, river impoundments, or possible commercial over-collecting as causes for apparent species decline. Later, Dodd et al. (1986) surveyed only ten locations, describing possible declines in the species for the same reasons cited above, and found populations of heavily diseased turtles. In follow-up work Dodd (1988) found as much as 50% population loss in diseased populations and in 1990 estimated that the FMT may be extirpated from as much as 93.1% of historically suitable habitat; however, these estimates were based on a limited number (n = 10) of sampling locations.

Genetic introgression may also be contributing to the decline of the FMT. The species is thought to share a narrow hybrid zone with the closely related stripe-necked musk turtle (*Sternotherus minor peltifer*; Estridge, 1970; Iverson, 1977; Mount, 1981) in the North River drainage of the Black Warrior River (Fig. 1), although until now, this has been based solely on the existence of morphological intermediates with no genetic data to substantiate the claim. Additionally, some authorities (Iverson, 1977; Mount, 1981) suggested that hybridization between the two species is mediated through the lock and damn system on the Black Warrior River which impounds the river in many locations disrupting its natural flow and creating habitat that may be more suitable for stripe-necked musk turtles than FMTs, thus facilitating hybridization.

Here we assess the current status of a cryptic, narrowly endemic, and rare reptile that is believed to have experienced population declines and potential genomic contamination due to anthropogenic disturbance. We use DOM, historic and contemporary survey data, as well as genetic sampling of specimens to determine the current range of the species, assess extinction probabilities across populations, and evaluate the genomic integrity of the FMT and its possible introgression with closely related species.

2. Methods

2.1. Study species, distribution, and sampling methods

The FMT inhabits the Black Warrior River system above the Fall Line in north-central Alabama, USA (Fig. 1). Previous studies have shown that this species prefers creeks and rivers of intermediate size (≤ 3 rd order) and intermittent depths (1–5 ft) with primarily rocky substrate and either abundant flagstone or sandstone shelves that extend underwater for retreat sites (Estridge, 1970; Mount, 1981; Ernst et al., 1983). In addition to observed habitat preferences, laboratory based studies (Jackson, 1988) show that FMTs spend significantly more time wedged under sublittoral objects than other members of the genus. The distribution of the FMT is completely surrounded by that of the stripe-necked musk turtle, and the only likely route for hybridization between these species occurs in the Black Warrior River as it crosses the Fall Line (Fig. 1) for reasons described below. As the Black Warrior River passes through the Fall Line (the geomorphic division between the provinces of the Appalachian Highland and Gulf Coastal Plain; Fig. 1), river substrate becomes primarily sandy and the FMT is replaced by the stripe-necked musk turtle. Additionally, the stripe-necked musk turtle is found to the west in the Sipsey River, which is entirely within the Coastal Plain. The distribution of the FMT is also bound to the east and

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