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Confronting the invasive species crisis with metamodel analysis: An explicit, two-species demographic assessment of an endangered bird and its brood parasite in Puerto Rico

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ABSTRACT

Invasive species pose a significant threat to native species persistence worldwide. Effective invasives management requires a detailed understanding of the mechanisms by which they impact native taxa, yet most quantitative models used to inform management do not address these complex interactions. Populations of the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*, YSBL) have declined dramatically across southwestern Puerto Rico, largely through brood parasitism by the invasive Shiny Cowbird (*Molothrus bonariensis*, SHCO). YSBL management is focused on removing SHCO eggs from Blackbird nests and on constructing artificial nest structures (ANS) that are resistant to terrestrial predators and easily monitored for SHCO parasitism. Despite these efforts, successful recovery of YSBL requires a more thorough knowledge of the complex two-species system. We used a new "metamodel" approach to explicitly simulate demographic interactions between these two species. The metamodel featured two separate, individual-based demographic models running concurrently, with specific data-driven linkages simulating the species interactions and their impacts on population dynamics. Results indicated that YSBL management may be most effective by direct removal of SHCO eggs from parasitized nests, which can also reduce the number of fledged Cowbirds that subsequently prefer YSBL nests as adults. Fledging success and post-fledging survival, previously not considered serious threats, were also identified as critical determinants of YSBL population viability and important targets for management. Importantly, trapping of SHCO did not emerge as an effective method of YSBL management. This is among the first population viability simulation models featuring explicit, simultaneous treatment of linked demographic dynamics in a native-invasive species system.

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1. Introduction

The introduction of invasive species is widely considered to be a major cause of environmental and agricultural damage around the world (Pimentel et al., 2005), and is a factor that contributes to endangerment and extinction of many native species (Didham et al. 2005; Roberts et al., 2015). A number of modeling approaches have been described that inform natural resource managers on how to most effectively manage invasive species, where management is defined as minimizing the risk of future invasions and/or controlling existing invasive populations. These approaches range from simple elasticity analysis of matrix population models (e.g., Buhle et al., 2005) to sophisticated bio-economic models utilizing optimal control theory (e.g., Burnett et al., 2007; Fresard and Ropars-Collet, 2014) to identify biologically effective and economically efficient strategies for reducing invasive species populations and their impacts.

These approaches focus on the invasive species alone, without consideration of other species that may be at risk because of the invasion. In the context of conservation of endangered species threatened by invasive species, successful management of both the invasive and impacted endangered species is critically dependent on understanding the functional ecological and demographic relationships linking them. For those responsible for endangered species management, this two-species system becomes considerably more complex intellectually and more analytically challenging. At the same time, the damage done by an invasive species might be countered by management aimed at the endangered species, even if the invasive species cannot be controlled effectively.

An approach that is often applied to endangered species management is population viability analysis (PVA), which includes analytical

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techniques for evaluating quantitative impacts of threatening processes and identifying effective management strategies (Beissinger and McCullough, 2002; Morris and Doak, 2002). While considered a valuable tool for organizing information and systematically evaluating management options, PVA is often criticized for its single-species approach where interactions with other species are treated in a rather abstract manner, i.e., as modifiers to demographic rates in the focal species or as general sources of inter-annual environmental variability. This limitation is a significant impediment to using traditional PVA tools to study an explicit two-species system such as an endangered species impacted by an invasive species.

Recently, a new approach known as "metamodeling" (Lacy et al., 2013) was developed that allows conservation biologists to create more informative and holistic models of the threats acting on wildlife populations. The approach links discipline-specific models representing components of an overall system, with a central "facilitator" program controlling data sharing between individual models. This interactive data flow combines the methods and strengths of each discipline into a more encompassing analysis of main effects, interactions among effects, and emergent higher-level dynamics. Recent applications of the metamodeling approach address a broad range of wildlife conservation issues (Bradshaw et al., 2011; Prowse et al., 2013; Agostini et al., 2014; Shoemaker et al., 2014; Wells et al., 2015).

A system defined by a native endangered species threatened by an invasive species should be well-suited for analysis using a metamodeling approach. We report here on an explicit two-species metamodel featuring an endangered native species in Puerto Rico, the Yellow-shouldered Blackbird (*Agelaius xanthomus*, hereafter YSBL), whose future persistence is threatened by the invasive Shiny Cowbird (*Molothrus bonariensis*, hereafter SHCO). We explored the nature of the interactions between the species, and the demographic consequences of these interactions on the native species. We evaluated alternative management options directed at the endangered Blackbird and the invasive Cowbird, and we make recommendations for effective biological management of the system to improve the prospects for the endangered species recovery. To our knowledge, this is the first population viability simulation model featuring explicit, simultaneous treatment of the demographic dynamics of both an endangered species and the invasive species with which it interacts.

2. Materials and methods

2.1. Study system

The YSBL is endemic to Puerto Rico, with a subspecies located in Mona Island (*A. x. monensis*) that will not be considered in this analysis (Fig. 1). The YSBL was considered common and widespread in Puerto Rico until the 1940s, after which no information of the species was obtained until 1972 (Post and Wiley, 1976). Abundance in the early 1970s was estimated to be approximately 2200 individuals, concentrated primarily in southwest Puerto Rico with perhaps 200 individuals in the southeastern area of the island (Post and Wiley, 1976).

The SHCO is an avian brood parasite, laying its eggs in the nests of many host bird species and leaving the eggs to be raised by foster parents. Over the past century, the SHCO expanded its range northward from South America through the West Indies as forest clearing for agriculture created vast areas of preferred Cowbird habitat (Cruz et al., 2000). SHCO first inhabited Puerto Rico in the 1950s (Grayce, 1957) and was first recorded in western Puerto Rico in the late 1960s (Kepler and Kepler, 1970). The generalist species is now distributed throughout the island with total abundance measured in the tens of thousands (Medina-Miranda et al., 2013).

Between 1974–75 and 1981–82, the YSBL population in southwestern Puerto Rico declined by more than 80% to 300 individuals (USFWS, 1996). While Post and Wiley (1976) determined that the decline was caused by a number of factors, brood parasitism by SHCO was identified as the primary mechanism (Wiley et al., 1991). The YSBL was listed as an endangered species in 1976, with critical habitat designated in the same year (USFWS, 1976). More recently, introduction of rhesus macaque *Macaca mulatta* and patas monkey *Erythrocebus patas* may have further threatened YSBL populations.

In 1984, the Puerto Rico Department of Natural and Environmental Resources (PRDNER), in a cooperative agreement with the US Fish and Wildlife Service (USFWS) established the YSBL Recovery Project (USFWS, 1996). In coastal mangrove nesting habitats, Recovery Project staff monitor YSBL nests in natural substrates and in over 200 artificial nest structures (ANS). This monitoring includes the removal of SHCO eggs from YSBL nests and trapping and destroying adult SHCOs as approved annually by PRDNER and in accordance with ethical guidelines set forth by the American Veterinary Medical Association (AVMA,

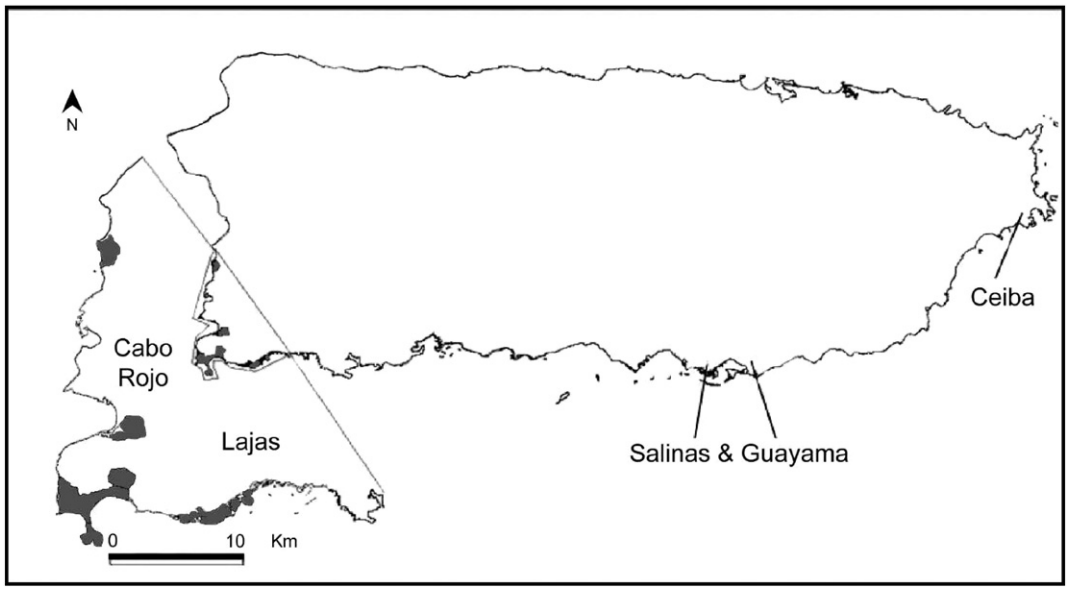

Fig. 1. Map of Puerto Rico showing the local distribution of the Yellow-shouldered Blackbird (*Agelaius xanthomus*) in dark gray. Isolated small populations in the southeast are indicated by region. Mona island population not shown. Distribution data adapted from Gould et al. (2008).

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