The role of social behavior in buffering populations from extinction: persistence of an endangered, cooperatively breeding passerine

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Summary
In small populations, aspects of species' behaviors are directly relevant to extinction risk. Small populations can be drawn into extinction vortices – positive feedback cycles leading rapidly to extinction. Social behaviors referred to as Allee effects accelerate the decline, but there is little work on how social behavior might buffer small populations against extinction risk. Our research is focused on understanding (1) how a species' social behavior might buffer extinction risk when populations are small, and (2) the viability and persistence of an endangered bird, the White-breasted Thrasher. The White-breasted Thrasher is a cooperative breeder – young from earlier nests forgo breeding to assist their parents in rearing the next generation of young – and we think that this social system might buffer extinction risk. Here we propose that cooperative breeding buffers the short-term population dynamics of the endangered White-breasted Thrasher after significant habitat loss. We tested our hypothesis by comparing demographic and behavioral data collected before, immediately after, and now five years after habitat loss. Nest success did not change significantly over time, with success rates of 37%, 31%, and 35% in the three time periods, respectively. A similar pattern was seen in other measures of reproductive success. Conversely, cooperative breeding behavior significantly increased after habitat loss. Although groups did become significantly larger, the increase in sociality was mainly driven by a shift from a population comprised largely of territorial pairs to one comprised largely of cooperative groups. Our results suggest that facultative cooperative breeders may be buffered from the negative demographic effects typically experienced in crowded populations after large-scale habitat loss. These results will aid in understanding the buffering capacity of social behaviors and ultimately lead to improvements in extinction risk assessments of small populations.

Background
Extinction risk is high in small populations because of stochastic (random) processes such as variation from year to year in the environment, such as in food availability. The risk of extinction is exacerbated by a suite of behaviors that are not a problem in larger populations, but become liabilities in small populations. For example, species with large territories can have difficulty finding a mate when numbers are low, there can be breakdown of group predator defenses, and some species require large numbers for social facilitation of mating or foraging – called Allee effects. These behavioral factors underpin recent attention to the broader importance of species behaviors to population persistence. Behaviors can, and arguably should, be included explicitly in models for predicting extinction risk, such as population viability analysis (PVA). Inclusion of behaviors that decrease variation in reproduction and survival increase population growth rate and improve model predictions. PVAs have become an important tool to aid in the conservation of imperiled species and have been employed in over 200 studies in the last 5 years. In contrast to Allee effects, which are regularly included in PVAs, very little attention has been paid to the possibility that some other social behaviors might actually ameliorate effects of population decline and help buffer a small population from extinction. One type of behavior that might buffer small populations from extinction is cooperative breeding, a social system in which adult offspring stay and help their parents raise offspring (their siblings) rather than breed on their own.

One mechanism by which cooperative breeding may reduce extinction risk is by minimizing density dependent feedback when adult numbers increase. This benefit contrasts with socially monogamous species, where an influx of refugees following habitat loss has been shown in some systems to lead to...
decreased reproductive success of the residents (Fig. 1).\textsuperscript{10,11} We have evidence that buffering actually occurs in the endangered cooperatively breeding White-breasted Thrasher (\textit{Ramphocinclus brachyurus}). Immediately following the loss of 41\% of available habitat over two years thrashers continued to occupy the remaining habitat in high densities, with more helpers but no decrease in reproduction.\textsuperscript{12} However, the longer term consequences of habitat loss on the behavior and viability of this endangered bird are unknown.

\textbf{Hypotheses}

We tested two hypotheses to integrate behavior and extinction risk. (1) The buffering of population persistence through increased family size and stable reproduction is maintained years after habitat loss. We tested this hypothesis by comparing demographic and behavioral data collected before\textsuperscript{12}, immediately after\textsuperscript{13}, and now five years after habitat loss. (2) Cooperative breeding social systems would exhibit the greatest population persistence, particularly for small populations, than will alternative mating systems (monogamy, types of polygamy). We tested this hypothesis by evaluating population persistence modeled for the cooperative breeding system exhibited by the thrashers compared to a suite of novel viability models encompassing the range of avian mating systems.

\textbf{Study Species}

The White-breasted Thrasher is endemic to the Caribbean islands of St. Lucia and Martinique, and there are approximately 600 breeding pairs in total. In 2005, one-third of the species habitat was destroyed or disrupted by resort developers. Our fieldwork took place in and around the development during the 2011 thrasher breeding season (June-August). The thrasher as an excellent study species for questions about social behavior and extinction risk because (1) it has a restricted distribution to two small Caribbean islands, and thus anticipating and preventing its extinction is important, (2) its range was recently reduced due to habitat loss, (3) it is a facultative cooperative breeder (groups are composed of 2 breeders and 0-4 helpers), and (4) demographic data exist from before and immediately after habitat loss.

\textbf{2011 Accomplishments}

\textbf{Nest searching and monitoring} – Thrasher nests are conspicuous and often in the same location year to year; our approach consisted of searching habitat for nests, using a combination of GPS coordinates of previous nest sites and systematic searches (Fig. 2). Thrashers re-nest after failed attempts, and they will attempt 2\textsuperscript{nd} and 3\textsuperscript{rd} broods after successful breeding, so nest searching occurs throughout the entirety of the breeding season. We gathered breeding-season data on White-breasted Thrasher cooperative breeding behavior, reproductive success, and survival at 63 nests (Fig. 3).
Measuring reproductive success – We determined components of reproductive success, e.g. clutch size, hatching success (% of eggs that hatch), fledging success (% of chicks that jump out of the nest), and total nest survival, by monitoring nests every three days. Nest visits were more frequent when hatching and fledging were imminent. We calculate daily nest survival with the logistic-exposure method, a generalized linear model used when studying populations with varying exposure periods.14

Assessing survival – In order to document thrasher survival, at each nest, we captured, banded, and aged birds not already banded. We captured birds in mist nets and chicks at the nest and banded each with a unique combination of leg bands. Banding allowed us to identify individual birds in subsequent years, as well as to determine social group sizes and social roles. We monitored thrasher survival by resighting birds banded in previous years (> 400 banded since 2002), and estimated survival using Program MARK.15 We banded 81 thrashers and re-sighted 29 that had been banded immediately before and immediately after habitat loss.

Measuring cooperative breeding behavior – Measurement of group composition requires knowing the identity of individual birds. After capturing and banding thrashers at a subset of nests, we performed focal nest surveys to record all individuals and activities at the nest. We used a standardized sequence of recorded thrasher calls to lure birds into the area. Determining group size is not trivial and requires multiple visits to determine if the territory has 2 adults, 3 adults, 4 adults, etc. Additionally, because thrashers are sexually dimorphic, they cannot be sexed in the field. We collected up to 50 μl of blood from each individual for extraction and sex determination at Tufts.

Population modeling – We are currently using the data acquired on St. Lucia to construct a White-breasted Thrasher population viability analysis (PVA) using an individual-based model in MATLAB, which will allow for greater sophistication in model structure as compared to using commercially available PVA programs. In addition, we are modifying this custom-built computational model for evaluations of how social behavior affects extinction risk.
Results

Results from this work are being prepared for publication and will be available from TIE when published.

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Literature Cited