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NEWS AND VIEWS

PERSPECTIVE

Extinction, reintroduction, and restoration of a lizard meta-population equilibrium in the missouri ozarks

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In this issue of Molecular Ecology, Neuwald & Templeton (2013) report on a 22-year study of natural populations of Collared Lizards (Crotaphytus collaris) that evolved on isolated on rock outcrops ('glades') in the Ozark Mountains in eastern Missouri. This ecosystem was originally maintained by frequent fires that kept the forest understory open, but fire-suppression was adopted as official policy in about 1945, which led to a loss of native biodiversity, including local extinctions of some lizard populations. Policies aimed at restoring biodiversity included controlled burns and re-introductions of lizards to some glades, which began in 1984. Populations were monitored from 1984–2006, and demographic and genetic data collected from 1 679 lizards were used to documents shifts in meta-population dynamics over four distinct phases of lizard recovery: 1–an initial translocation of lizards drawn from the same source populations onto three glades that were likely part of one meta-population; 2–a period of isolation and genetic drift associated with the absence of fires; 3–a period of rapid colonization and population increase following restoration of fire; and 4–stabilization of the meta-population under regular prescribed burning. This study system thus provides a rare opportunity to characterize the dynamics of a landscape-scale management strategy on the restoration of the meta-population of a reintroduced species; long-term case studies of the extinction, founding, increase, and stabilization of a well-defined meta-population, based on both demographic and population genetic data, are rare in the conservation, ecological, and evolutionary literature.

Keywords: conservation genetics, population dynamics, population genetics–empirical, reptiles, wildlife management

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The Missouri Ozarks were originally covered by deciduous forest in which desert-like glades developed on the driest ridge tops and are characterized by xeric communities typical of south-western US hot deserts ('prickly pear' cactus, scorpions, tarantulas, etc.) in which the carnivorous collared lizards (Fig. 1) are top predators. These island lizard populations have been isolated on the periphery of the main distribution of the species (south-western North American deserts) for about 4 000 years, and the glades were historically maintained by low-intensity fires that occurred on average every ~5 years (Templeton *et al*. 2001). Although individual glades may be very small and support only tiny lizard populations, genetic data suggest that they were likely interconnected by dispersal of lizards from nearby glades and were maintained as meta-populations by recurrent gene flow (Hutchison & Templeton 1999). This equilibrium between extinction and recolonization could be maintained so long as the burns kept forest understories open enough to permit occasional lizard dispersal.

European settlement of this region was accompanied by clear-cutting of most of the region's original forest, and then another round of logging of second-growth forests. In 1945, the Missouri Department of Conservation (MDoC) purchased 9 300 ha of land in the eastern Ozark region, which had been subject to extensive degradation since the 1800s. This land became the Peck Ranch Conservation Area (PRCA) and was managed under a conservation policy of woodland fire suppression. This policy fostered regrowth of dense forest between glades, and invasion of the glades themselves by woody vegetation, which then both restricted lizard dispersal and reduced lizard habitat, respectively. Thus, a policy of fire suppression resulted in fragmentation of glade microhabitats by eliminating lizard dispersal and disrupting gene flow, thereby increasing the loss of genetic variation within local demes, while increasing local extinctions (Templeton *et al*. 2007, 2011). This deme-by-deme 'extinction ratchet' played out across this part of Missouri, and by 1980, ~75% of the collared lizard populations in the eastern Ozarks had become extinct, and none could be found on or near the PRCA (Templeton 1982).

In 1982, the MDoC initiated a lizard translocation programme to reverse these local extinctions, which included burning woody vegetation that had invaded glade habitats in the absence of fire and moving 29 lizards on to three different glades on Stegall Mountain within the PRCA in 1984–89 (Fig. 2). These reintroductions were staggered, with 10 lizards released on glade SM-7 in 1984, 9 more on SM-8 (1987) and 10 more on SM-9 (1989; Fig. 2). The controlled burns of the glades kept these open, but they were still isolated by unburned dense forest, and there was no evidence of any dispersal between glades SM-7

Fig. 1 Adult male collared lizard (Crotaphytus collaris) from an isolated population in the 'glades' region of the Ozark Plateau of eastern Missouri. This adult male is part of a glade population on Bell Mountain, about 50 miles from the Peck Ranch, and from which large yearlings were taken for translocation the Stegall Mountain study area (photo by Dr. Alan R. Templeton, May 1984).

and SM-8, which were separated by only 50 m! To restore dispersal as well as maintain open glades, the MDoC initiated woodland burning in 1994 over an area that included both of these glades, and later, the burn area was extended to cover all of Stegall Mountain and at that point also included glade SM-9 (Fig. 2).

Founder populations for these three glades were made up of lizards from the same 4–5 different source glades, so that all were initially characterized by similar levels of genetic variability. Prior to these reintroductions, little or no genetic diversity existed within local demes remaining in the Ozarks, but there were fixed differences between demes (Hutchison & Templeton 1999), so all three glades on Stegall Mt. were characterized by high levels of initial diversity. Mark–recapture data revealed that no lizards colonized new glades within the first decade (1984–93), confirming that glade restoration *per se* did not restore meta-population dynamics. In 1994, the prescribed burns were expanded to include forest surrounding the glades, and lizards showed immediate responses to new fire regimes: dispersal increased as did the colonization of unoccupied glades, individual population sizes increased, and by 2000, the meta-population on Stegall Mt had stabilized with respect to total population size, number of glades occupied and the extinction/recolonization dynamics of local demes.

Field work required monitoring of glades annually beginning with the reintroductions in 1984, and continuing to 2006, with all individuals identified by a unique number (via toe clip). Local populations were defined by the boundaries of each glade, and because these were usually small and closed, sampling often included 80–100% of the total number of lizards present. Six microsatellite loci (Hutchison *et al*. 2004) were sufficient to identify every individual, and new regression statistics were derived to accommodate small sample sizes and auto-correlation of data through time (via year-to-year survival of some individuals within a local population) and to weight each population by its harmonic mean size over the study period.

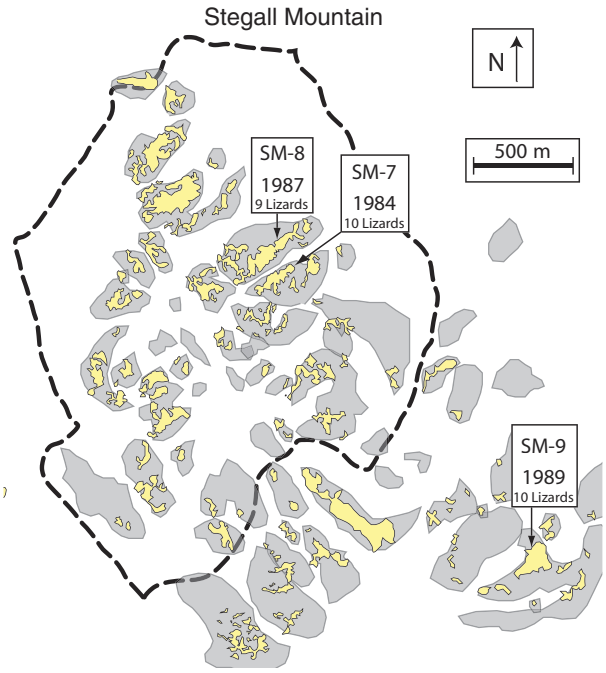

Fig. 2 Map of the Stegall Mountain study area, showing the original extent of the glades (grey shading), and the reduced glades habitats (yellow) after encroachment by woody vegetation as a result of fire suppression. Each of the three glades on which lizards were introduced is identified, with the year of introduction and the number of individuals translocated. All founders were drawn from the same 4–5 off-site source populations, and the irregular dashed line shows the burn area initiated in 1994.

The genetic data revealed temporal changes in genetic drift, genetic diversity and between-population divergence over the 22-year period characterized by major changes in meta-population demographic history (associated with elimination & then restoration of fire regimes).

Demographic and genotypic data revealed four distinct temporal stages of the recovery process. First, founder populations revealed a deficiency of heterozygotes in 17% of the tests in year 1, reflecting the expected Wahlund effect from introductions of individuals from glades fixed for different alleles. This effect dropped to 1.2% in subsequent years, a pattern consistent with random mating within individual glades. The second demographic phase of this study, the 'fire- suppression' period, followed the three founder populations which all began with a similar number of individuals (Fig. 2) and with similar levels of genetic diversity and allele frequencies. Despite similar starting conditions, the three populations experienced different genetic histories but shared several common features: all showed a decrease in within-population genetic diversity, a drop in allele numbers and a differentiation from each other. These are all signatures of strong genetic drift within each of the three demes due to an almost complete absence of between-population dispersal until prescribed burning began.

Expansion of prescribed burning from the glades to the surrounding forest initiated the third demographic phase

(colonization) at Stegall Mountain, and mark–recapture data revealed that most colonizers were yearlings that hatched the year prior to their dispersal. Genotyping of all marked individuals on all three glades allowed strong inferences about 'glade of origin' for the majority of colonists because most carried private alleles that matched single source glades. The fourth distinct phase in this study was the transition to a 'demographically stable' meta-population structure characterized by interconnected local populations. Here, among-glade differentiation declined, and there were too few private alleles to track dispersal in most cases.

This study has provided a unique opportunity to document the history of a meta-population from extinction through full restoration, in a system in which all founders, their genotypes, and their source populations are known, and the founders were chosen to maximize genetic diversity of the translocated populations in the recovery effort. There have been spectacular cases of 'genetic rescue' of individual populations, such as the case of the Florida panther (Johnson *et al.* 2010), but I am unaware of a landscape-scale case study on restoration of a meta-population. Lizards have served as 'model organisms' for study of a broad range of ecological and evolutionary questions (Pianka & Vitt 2003; Losos 2009; Camargo *et al.* 2010), and now we can add restoration of meta-population dynamics to this distinguished research history. The lessons learned here are likely to be applicable to larger scale efforts at maintaining or restoring corridors to conserve meta-populations of apex predators, pollinators and seed dispersers, and migratory animals (Hilty *et al.* 2006; Fraser 2009; Beckman *et al.* 2010), at both regional (www.florida wildlifecorridor.org) and even continental scales (y2y.net; http://www.panthera.org/programs/jaguar/jaguar-corridor-initiative; A compendium of existing and planned Australian wildlife corridor projects and initiatives, and case study analysis of operational experience).

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J.W.S., Jr., has conducted research in phylogenetics, phylogeography, hybrid zone dynamics, origins of parthenogenesis, species delimitation, and population/conservation genetics of non-avian reptiles (primarily lizards) for 35 years, and learned the basics of restriction-mapping during a short-term leave in A.R.T.'s lab in 1986. Regrettably A.R.T. was on leave at the Univ. of Michigan and the two did not overlap, but Sites nevertheless was introduced very early to the beginning stages of this long-term study by the Templeton group. The invitation to write this perspective was an honor and a joy, and a visit to the now "hallowed ground" of the Peck Ranch glades is now on Sites' "bucket list".

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