Augmentation Provides Nominal Genetic and Demographic Rescue for an Endangered Carnivore

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Abstract
Augmentations are used frequently to restore populations of conservation concern. Carnivores, in particular, are often targeted for augmentations, yet quantitative assessments of these efforts are rare. In Wisconsin, USA, American martens were reintroduced and subsequently augmented, yet remain state endangered. To evaluate this restoration effort, we sampled martens before and after augmentation, used genetic mark-recapture and parentage analyses to quantify stage-specific vital rates for each step of the augmentation, and assessed demographic viability with and without augmentation. Surprisingly, augmentation provided minimal genetic and demographic contributions, and persistence was instead driven by intrinsic population attributes such as recruitment. Our findings question augmentation as a primary restoration strategy for carnivores, and we urge conservation practitioners to focus on identifying and enhancing limiting population processes such as immigration and juvenile survival prior to using costly and controversial measures like augmentation.

Introduction
The intentional movement of animals to re-establish extirpated populations or to augment declining ones is an important tool for conservation biologists (Seddon et al. 2014). Despite constituting up to a third of all translocation attempts, augmentations have received little attention, and the vast majority go unmonitored and unassessed (Wolf et al. 1996; Gusset 2009). Moreover, while there has been high profile success in rescuing genetically depauperate (e.g., Florida panther [Puma concolor coryi]; Johnson et al. 2010) and critically small populations (e.g., African wild dog [Lycaon pictus]; Gusset 2009), translocated individuals often fail to contribute to recovery (Arrendal et al. 2004; Champagnon et al. 2012). Consequently, the use of augmentation as a conservation strategy has been questioned (Macdonald 2009; Champagnon et al. 2012).

Due to their extensive top down effects (Estes et al. 2011), mammalian carnivores are of particular conservation concern, and among the most frequently translocated species (Seddon et al. 2005). Unfortunately, the continued decline of carnivores has necessitated calls for enhanced restoration efforts (Ripple et al. 2014), yet, translocations tend to be prolonged events that are both costly and controversial (Gusset 2009). Moreover, due to their slow life histories, large home ranges, and low population densities, carnivores have proven difficult to repatriate. Nevertheless, augmentation can be effective in some cases (Vinkey et al. 2006; Powell et al. 2012). The American marten (Martes americana) is a small-bodied furbearer and the most commonly translocated carnivore in North America (Powell et al. 2012). Indeed, martens have been translocated > 50 x across 16 states and 6 Canadian provinces, dating as far back as the 19th century (Powell et al. 2012). Accordingly, the limitations to establishment and persistence are well-known (Powell et al. 2012). Moreover, martens possess all the aforementioned characteristics that hinder carnivore translocations. These shared life history attributes...
coupled with a detailed knowledge of translocation success make martens a model species to assess population augmentation in carnivores.

Following European colonization, martens were extirpated from much of the Great Lakes region, but populations have been re-established in several states (Williams et al. 2007). In Wisconsin, however, martens remain state endangered despite decades of restoration efforts, including the translocation of 139 individuals (139M, 45F) from the Superior National Forest in Minnesota to the Chequamegon National Forest (hereafter Chequamegon) between 1987 and 1990 (Williams et al. 2007). While a small population was established, recovery was not achieved and the population was augmented with 90 additional Superior martens (55F, 35M) between 2008 and 2010 in an attempt to stimulate population growth (Woodford et al. 2013). Evidence suggests that this population remains limited (McCann et al. 2014; Manlick et al. in review), but a rigorous assessment of augmentation has not been conducted for either restoration attempt.

In collaboration with state, federal, and tribal agencies, we developed a program to assess carnivore restorations, and monitored the Chequamegon marten population through the augmentation. Specifically, we used longitudinal genetic sampling to characterize the population through time and genetic parentage analyses to quantify the genetic and reproductive contributions of translocated individuals. We then used noninvasive sampling and genetic mark-recapture models to quantify stage-specific vital rates, and employed these empirical estimates to populate demographic models and quantify the impact of augmentation on population persistence. This approach not only provided a complete assessment of marten recovery in our system, but also presents a framework for future efforts to evaluate augmentation success.

Methods

Genetic analyses

Genetic data were compiled for three temporally discrete cohorts of Chequamegon martens: (1) the remnant population present before augmentation (hereafter, “resident” martens); (2) individuals translocated to Chequamegon; and (3) contemporary martens (i.e., post-augmentation) noninvasively sampled using a robust design framework (see Supporting Information). DNA was extracted from tissue, hair, and scat samples, and we used 14 microsatellite loci in conjunction with a species-specific SRY marker to identify the sex and individual identity of noninvasively collected samples (see Supporting Information). Resident and translocated individuals were genotyped at 14 loci with sex identified at capture. We quantified genetic variability by testing for linkage disequilibrium (LD), deviations from Hardy–Weinberg equilibrium (HWE), and local inbreeding ($F_{IS}$) using the program Genepop (Rousset 2008) with a sequential Bonferroni correction.

Vital rates

We quantified reproductive contributions from translocated individuals using parent-pair analyses with known sexes in program CERVUS (Marshall et al. 1998; Kalinowski et al. 2007). We employed standard likelihood approaches, used likelihood of difference scores to assign parentage, and applied a genotyping error rate of 0.07 (see Supporting Information). We assigned parentage to parent–offspring pairs using both strict (95%) and relaxed (80%) confidence levels, and to individuals in parent–offspring triads exceeding 80% confidence.

To estimate juvenile survival ($\phi_i$), we employed Pradel robust design models (Pradel 1996) using capture histories generated from noninvasive sampling of contemporary martens. In addition to estimating standard robust design parameters, Pradel models reverse capture histories to estimate per capita recruitment ($f$ – new individuals per existing individual) and realized population growth rate ($\lambda$; Nichols et al. 2008). Because marten parturition occurs in spring and we sampled in winter, all juvenile martens present during sampling were entering the yearling stage class, thus precluding our ability to model $\phi_i$ directly. Estimates of recruitment from Pradel models, however, allow for a derivation of $\phi_i$ since recruitment can be expressed as

$$f_i = b_i \cdot \phi_i + i_i,$$

where $b_i$ is the seasonal birth rate (i.e., number of juveniles per adult) and $i_i$ is the seasonal immigration rate. Because Chequamegon martens are isolated (Williams & Scribner 2010), we assumed no immigration, estimated juvenile survival as

$$\phi_i = \frac{f_i}{b_i},$$

and calculated variance using the delta method (Powell 2007). We employed the Pradel survival and recruitment parameterization in program MARK (White & Burnham 1999), and developed four a priori models (Table 1) to avoid overfitting (Fieberg & Johnson 2015). Limited capture histories did not all allow for incorporation of covariates or fully time-dependent models, and we assumed a constant population with no behavioral responses (i.e., $p = c$). Models were ranked using Akaike’s Information Criterion corrected for small sample size ($AIC_c$).
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Table 1  Mark-recapture models and associated hypotheses used to estimate vital rates

| Model                                           | Hypothesis                                                      |
|-------------------------------------------------|-----------------------------------------------------------------|
| $\phi, f, p = c.$                               | Constant survival, recruitment, and capture/recapture probability|
| $\phi, f, p_{\text{season}} = c_{\text{season}}$ | Constant survival and recruitment with seasonal variation in capture/recapture probability|
| $\phi_{\text{season}}, f_{\text{season}}, p = c.$ | Seasonal variation in survival and recruitment with constant capture/recapture probability|
| $\phi_{\text{season}}, f_{\text{season}}, p_{\text{season}} = c_{\text{season}}$ | Seasonal variation in survival, recruitment, and capture/recapture probability|

Figure 1  (a) Life-cycle diagram with vital rates and parenthetical variance used in demographic analyses of American marten augmentation. Model was female-based, assumed a birth pulse, and included juvenile ($J = \text{age 0–1}$), yearling ($Y = \text{age 1–2}$), subadult ($SA = \text{age 2–3}$), and resident adult ($A = \text{age 3+}$) stage classes, as well as two stages for translocated individuals ($T1 = \text{translocated propagule}$; $T2 = \text{surviving individuals 1-year post-translocation}$). Transitions denote survival ($\phi$) and fecundity ($F$), and values within each node denote the estimated number of females per stage class at time of augmentation. (b) Sensitivities ($s_{ij}$) and elasticities ($e_{ij}$) for each transition.

Demographic matrix models

We employed a female only, stage-based matrix model to quantify the population viability of Chequamegon martens before and after augmentation. We implemented a postbreeding survey, assumed a birth pulse with $t_0$ at parturition, and populated each transition using our empirically derived vital rate estimates or local estimates drawn from previous research (Figure 1a).

Stage-specific estimates of marten fecundity were acquired from the donor population in Minnesota (Erb et al. 2013) and were calculated as the product of stage-specific pregnancy rate, annual survival, and maternity (i.e., mean female kits per female, assuming an even sex ratio). Variance was estimated using the delta method. Yearling marten fecundity and variance was unavailable and was therefore scaled proportionally to subadult fecundity using the expected ratio between stage classes (Buskirk et al. 2012). Fecundity and variance of the translocated stage classes were calculated using the pregnancy rate and maternity of resident adults scaled proportionally to the percentage of translocated females assigned maternity in parentage analysis.

We estimated $\phi_J$ using Equation (2) and calculated $b_i$ as the average number of female kits per female using estimates from Minnesota (Erb et al. 2013), with variance estimated using the delta method. Given the assumptions in our derivation of $\phi_J$, and the uncertainty surrounding juvenile recruitment in martens (Schneider & Yodzis 1994; Buskirk et al. 2012), we also buffered our estimate using two extremes ($\phi_J = 0.25$ and $\phi_J = 0.50$; Schneider & Yodzis 1994). Variance of the high and low extremes...
was applied proportional to the error of our estimated $\phi$. We used known fate estimates of survival (McCann et al. 2010) for all non-juveniles and assumed adult, subadult, and yearling survival were equal (Buskirk et al. 2012). Because known fate survival estimates lacked seasonal estimates of variation (McCann et al. 2010), we were unable to isolate process variance. We used 200-day estimates of survival and variance for all translocated individuals (Woodford et al. 2013) because population augmentation occurred in the fall (i.e., 6 months prior to the birth pulse), and assumed survival of translocated individuals increased to that of resident adults after year 1 (Figure 1a). Population-specific correlations in vital rates were unavailable and not included.

To quantify the demographic consequence of augmentation, we employed deterministic matrix models and calculated vital rate sensitivities and elasticities for a population at equilibrium. To assess future viability we ran stochastic projections with and without augmentation using the package popbio in R (Stubben & Milligan 2007). We simulated 1,000 populations forward 50 years and employed an extinction threshold of 20 individual martens (Schneider & Yodzis 1994). The initial population size at the time of augmentation is uncertain, but Williams et al. (2007) approximated the Chequamegon marten population at 40 individuals. Thus, we assumed an equal sex ratio and populated the juvenile through adult stage classes with 20 individual females. McCann et al. (2010) reported only 0.15 juveniles per adult, therefore each model distributed 15% of the initial population to the first stage, and we allocated the remaining individuals proportionally among the adult (45%), subadult (15%), and yearling (25%) stages using a stable stage distribution (Figure 1a; Buskirk et al. 2012). Simulations including augmentation populated the initial translocation stage (i.e., T1) with 55 females (Woodford et al. 2013).

**Results**

**Genetic analyses**

We obtained genotypes for 51 resident martens (19F, 30M, 2 unknown) and 68 of 90 translocated individuals (33F, 35M). We noninvasively collected 75 contemporary marten samples and identified 37 unique individuals (21F, 12M, 4 unknown). Two samples were assigned to individuals despite allelic mismatch because they were identical at 13 of 14 loci and captured at the same location. We did not detect significant LD in resident or translocated individuals, nor did we detect deviations from HWE in the known resident population, but 4 loci in the translocated marten population deviated from HWE (Table 2). Contemporary individuals deviated from HWE at all loci and exhibited significant LD among 6 pairs. Contemporary martens also exhibited an extremely high inbreeding coefficient ($F_{IS}$), while the translocated population exhibited an inbreeding coefficient more than an order of magnitude higher than the resident martens (Table 2). Similarly, resident martens exhibited the highest observed heterozygosity while contemporary martens exhibited the lowest (Table 2). We assigned parentage to 13 offspring at 95% confidence, 3 offspring at 80% confidence, and 2 offspring from parent–offspring triads with >80% confidence. Despite this generous assessment, only three translocated females (17%) and three translocated males (17%) were assigned parentage (Figure 2; see Supporting Information).

**Mark-recapture models**

Of the 37 unique individuals sampled from 2012–2014, 31 were derived from hair snares and included in mark-recapture models. The top model held over 90% of the weight (Table 3), and indicated that survival and recruitment were constant over time while capture-recapture probabilities were equal but seasonally variable (see Supporting Information). Based on this model the population was stable ($\hat{\lambda} = 1.02; \text{SE} = 0.25$), recruitment was 0.57 (SE = 0.24), and we derived $\phi$ as 0.39 (SE = 0.21). Model ranks were robust to variation in $c$.

**Demographic models**

Deterministic matrix models showed that adult survival was the most elastic vital rate ($e_{AA} = 0.34$), while juvenile survival was the most sensitive ($s_{YF} = 0.53$; Figure 1b).

| Table 2  | Summary of genetic diversity in resident, translocated, and contemporary American martens in the Chequamegon National Forest |
|----------|-------------------------------------------------------------------------------------------------|
| Cohort   | N       | Alleles | $H_O$  | $H_E$  | HWE | LD | $F_{IS}$ |
| Resident | 51      | 5.64    | 0.59   | 0.58   | 0   | 0  | 0.01    |
| Translocated | 68      | 6.7     | 0.55   | 0.63   | 4   | 0  | 0.15    |
| Contemporary | 31      | 8.0     | 0.48   | 0.74   | 14  | 6  | 0.42    |

*N* = number of alleles; $H_O$ = observed heterozygosity; $H_E$ = expected heterozygosity; HWE = markers out of Hardy-Weinberg equilibrium; LD = marker pairs with linkage disequilibrium; $F_{IS}$ = Wright’s inbreeding coefficient.
Stochastic models suggested augmentation had minimal effects on population persistence, reducing the 50-year extinction probability by 12%, 17%, and 15% in the low (\(\phi_J = 0.25\)), estimated (\(\phi_J = 0.39\)), and high (\(\phi_J = 0.50\)) recruitment scenarios, respectively (Figure 3c). Nevertheless, augmentation did reduce extinction probabilities by up to 40% in the 6 years following translocation (Figure 3c). Long-term persistence was instead contingent upon juvenile survival as we detected up to a threefold difference in extinction probabilities between the high and low recruitment scenarios (Figure 3).

**Discussion**

We found that translocated martens provided nominal genetic and demographic contributions following augmentation, and persistence was instead driven by juvenile and adult survival. Given that adult survival is high (McCann *et al.* 2010), it has been hypothesized that low juvenile recruitment from nutritional limitation (Carlson *et al.* 2014) and enhanced competition (Manlick *et al.* in review) is inhibiting Chequamegon marten recovery. Our models supported this hypothesis with juvenile survival being the most sensitive vital rate and recruitment having stronger effects on population persistence than augmentation. While we derived a moderate estimate of recruitment for martens (Schneider & Yodzis 1994), our observed genotyping error rate could have inflated the number of new individuals and overestimated recruitment. If so, Chequamegon martens may be more at risk than predicted under our best estimate (Figure 3). In contrast, high levels of recruitment offset extinction probabilities in our models; however, we were unable to identify the proximate source of new individuals because immigration was removed from our derivation of juvenile survival and all recruitment was assigned to natal sources. Thus, future efforts should quantify immigration in order to identify and manage sources of recruitment. Nevertheless, we consistently provided optimistic demographic estimates throughout our analyses and these results indicate that the future viability of Chequamegon martens remains tenuous despite augmentation.

A key component of augmentation is that translocated individuals contribute reproductively to the recipient population. Despite the large number of individuals released and a generous assignment of parentage for both sexes, our analyses revealed minimal reproductive contributions from translocated individuals. In other translocated carnivores, reduced fecundity has been attributed to high mortality or long-distance dispersal of individuals following release (Moehrensclager & Macdonald 2003), yet, survival and establishment of residency were high in our population and did not vary significantly between ages or sexes (Woodford *et al.* 2013). Moreover, forested habitat appears sufficient (71011.6 ha; Figure 2; see Supporting Information), augmentation occurred at the optimal release time (Facka *et al.* 2016), and protocols followed best management practices, including both hard and soft releases, a large number of individuals, high male–female and juvenile–adult ratios, and multiple release sites over multiple years (Powell *et al.* 2012; Woodford *et al.* 2013). Consequently, our results suggest individuals from the augmentation either failed to reproduce or produced offspring with high mortality.

Like many carnivores, fecundity is the least influential vital rate for martens (Buskirk *et al.* 2012) and may not be expected to drive population restoration. Instead, genetic contributions of translocated individuals can be more important, particularly when augmenting small populations (Frankham 2009). We found that the translocated cohort had lower heterozygosity and higher inbreeding coefficients than did the resident population, a phenomenon that has led to reduced genetic variability in other carnivores (Arrendal *et al.* 2004). We observed a similar pattern among contemporary martens, though a high number of first order relatives (i.e., parent–offspring pairs) among these samples (Figure 2) likely inflated estimates of inbreeding and underestimated observed heterozygosity. Thus, while augmentation likely had no deleterious genetic consequences, the translocation of martens to Chequamegon does not appear to have provided positive genetic contributions either.

Critically evaluating translocations requires the assessment of both establishment and persistence.
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Figure 2 Location of the Chequamegon and neighboring National forests supporting American marten populations. Inset study area illustrates available habitat, known distribution of resident martens prior to augmentation, release sites for translocated individuals, distribution of hair snares used in contemporary sampling, and locations of contemporary marten captures. Locations of reproductive females are circled, and translocated females who produced offspring but were never recaptured are represented by their release locations. Lines connect mother–offspring pairs, and overlapping points are offset.

Figure 3 Cumulative extinction probabilities under varying levels of juvenile recruitment ($\phi_j$) with (a) and without (b) augmentation, and the reduction in extinction probability due to augmentation (c). All models assumed a starting population of 20 individual females and used an equivalent extinction threshold.

(Seddon 1999). Establishment is generally characterized by the survival and reproduction of translocated individuals (Gusset 2009), and while the former was high in our study (Woodford et al. 2013), reproductive contributions were limited. Nevertheless, augmentations are designed to supplement established populations and it is more appropriate to evaluate persistence. Our findings show that augmentation had limited effects on future viability, indicating that the recovery of Chequamegon martens has not been achieved. Given that martens possess traits characteristic of most solitary carnivores, our results indicate augmentation may not be an effective restoration strategy for other threatened carnivores with similar life histories. Consequently, augmentation should
be reserved for populations that exhibit significant inbreeding depression (i.e., genetic rescue; Johnson et al. 2010) or small populations that are subject to Allee effects (i.e., demographic rescue; Somers et al. 2008), particularly in social species. Indeed, Decesare et al. (2011) found that augmentations were incapable of reviving critically small populations unless subject to positive density dependence, and while Bouzat et al. (2009) did observe immediate benefits from genetic rescue, they maintained that persistence is ultimately contingent upon reversing the causal agents of decline rather than artificially reinforcing populations through augmentation. Thus, though augmentations may reduce short-term extinction probability (Figure 3c), long-term persistence is likely unachievable unless the limiting population processes or environmental factors are addressed (Bouzat et al. 2009; Decesare et al. 2011).

Augmentations are frequently used to restore carnivore populations, yet documented success is rare (Macdonald 2009). Coupled with the costs (Lindsey et al. 2005) and public perceptions surrounding carnivore augmentation (Austin 2004), we argue that long-term monitoring and management of intrinsic population attributes can be a more effective strategy. For example, our results indicate high levels of recruitment offset extinction probabilities more substantially than augmentation, indicating management should enhance juvenile survival. However, previous monitoring has revealed that Chequamegon may be resource limited, thereby rendering the enhancement of natal recruitment through environmental manipulations unfeasible (Carlson et al. 2014; Manlick et al. in review). Thus, we promote improving connectivity to established marten populations in the neighboring Nicolet and Ottawa National Forests (Figure 2) in order to enhance recruitment through immigration, and we suggest others take a similarly pragmatic approach to species restoration.

It is imperative that conservation practitioners evaluate the processes limiting population recovery prior to employing costly and controversial measures like augmentation. Indeed, this study underscores the importance of such assessments and highlights the remarkable amount of data needed to quantify limiting population processes. Thus, we encourage multiagency collaboration and long-term monitoring to enable both the characterization of population processes and the thorough assessment restoration strategies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s web site:

Table S1. Microsatellite summary statistics for all analyzed samples (N_{total} = 156).

Table S2. Mother-offspring pairs and parent-offspring triads assigned parentage at > 80% confidence.

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