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TECHNICAL NOTE

Detecting population recovery using gametic disequilibrium-based effective population size estimates

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Abstract Recovering populations often must meet specific growth rate or abundance targets before their legal status can be changed from endangered or threatened. While the efficacy, power, and performance of population metrics to infer trends in declining populations has received considerable attention, how these same metrics perform when populations are increasing is less clear. We examined the ability of a one-sample effective population size (N_e) estimator (LDNe) to discriminate between stable and increasing population trends across varying sample and initial population sizes. The performance of LDNe was compared to the Lincoln-Peterson (LP) abundance (N) estimator. The ability to identify stable and increasing populations varied widely across sample sizes and number of generations between sequentially collected samples, but LDNe outperformed LP. One-sample N_e estimates show promise as an efficient method of detecting population increase when samples of 60–120 individuals are collected 5–10 generations apart.

Keywords Abundance · Effective population size · Genetic monitoring · Population recovery · Population trend

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Identification of vulnerable populations is often followed by efforts to promote population recovery (Marsh and Trenham 2008). Recovery efforts often have limited resources, so inexpensive indicators of population status are especially useful. We explore monitoring of stable and recovering populations with N_e estimates inferred from the amount of gametic disequilibrium (LDNe; Waples and Do 2008) and N estimates generated from the LP mark-recapture of unique individual genotypes in a sample.

We used SimCoal (Laval and Excoffier 2004) to create multilocus allele frequencies for 100 replicate populations with historic $N_e \approx 1{,}000$ (Tallmon et al. 2010). For each replicate, a close approximation of a Wright-Fisher (W–F) population of size N was created with R package Rmetasim (Strand 2002), and individuals were assigned alleles from the distribution generated by SimCoal. Each population then went through a 10-generation equilibration phase of W–F mating at size $N = 100$, 250, 500, 1,000 to allow Hardy–Weinberg proportions and stable levels of gametic disequilibrium. Mutation was included at a rate of 10^{-3}/locus/generation.

Each of 100 replicates then followed a deterministic growth rate ($\lambda = 1.0$ or 1.1) for 11 generations starting at generation t_{-1}, and data were collected at t_0, t_1, t_5, and t_{10}. During this simulation phase, 30 unlinked loci were analyzed from samples of individuals ($S = 30$, 60, or 120) at specified times ($t = 0$, 1, 5, or 10) and used to estimate N_e, N, and λ. From each sample, $\hat{N}_e$ and $\hat{N}$ were obtained from individual genotypes using LDNe and LP estimators, respectively. Because LP N estimates are based on two samples, each S was sampled with replacement twice at S/2 to serve as the mark and recapture portions of the LP $\hat{N}$ estimates (Tallmon et al. 2010). For each method, $\hat{\lambda}$ was estimated as the slope of a linear regression on the log

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transforms of the point estimates of abundance at t_0 and t_i. In some replicates, $\hat{\lambda}$ was not estimated because an $\hat{N}_e$ was infinite or $\hat{N} = 0$. We assessed performance of the LDNe and LP methods by recording the proportion of times $\hat{N}_e$ or $\hat{N}$ estimates taken from sequentially collected samples produced $0.95 < \hat{\lambda} < 1.05$ when true $\lambda = 1.0$ (stable), and $\hat{\lambda} > 1.05$ when true $\lambda = 1.1$ (increasing).

The power to identify an increasing population was always lower than the power to detect a stable one for a given set of sampling constraints. Variability in $\hat{\lambda}$ obtained from both methods—based on either $\hat{N}_e$ (LDNe method) or $\hat{N}$ (LP method)—ranged from high for small sample, 1-generation trials, to much lower for larger samples and generation times (Fig. 1). In general, power was low (<0.60) if sample size was small ($S = 30$; Table 1). At larger samples sizes ($S = 60$–120) and 5–10 generations between samples $\hat{N}_e$- and $\hat{N}$-based $\hat{\lambda}$ began to distinguish $\lambda = 1.0$ from $\lambda = 1.1$ consistently (Fig. 1). At 10 generations between samples, the difference in peaks of $\hat{\lambda}$ frequency distributions became much more pronounced (Fig. 1).

Because the strength of genetic drift is larger at smaller population sizes, $\hat{N}_e$-based estimates of λ were much better at $N = 250$ or 100 than at 500 or 1,000, and improved as more generations passed between sampling events (see Table 1). $\hat{N}_e$ usually outperformed $\hat{N}$. At N = 500 or 1,000, the power of $\hat{N}_e$ and $\hat{N}$ to correctly identify the population growth rate was fairly low unless sample sizes were large (S = 120) and 5–10 generations passed between sampling events. At large sample sizes (S = 120), statistical power to detect population trends with $\hat{N}_e$ from samples taken 5–10 generations apart was much higher (>.70), except at the largest $N = 1{,}000$ (Table 1). In general, as other authors have noted, it is easier to detect declining populations than increasing ones (Tallmon et al. 2010).

In our simulations, the LDNe estimator detects increasing abundance over intervals of ≥5 generations between samples. Species with large numbers of individuals available for sampling (such as offspring) and short generation times, may lend themselves to monitoring with LDNe. Organisms with long generation times and a small

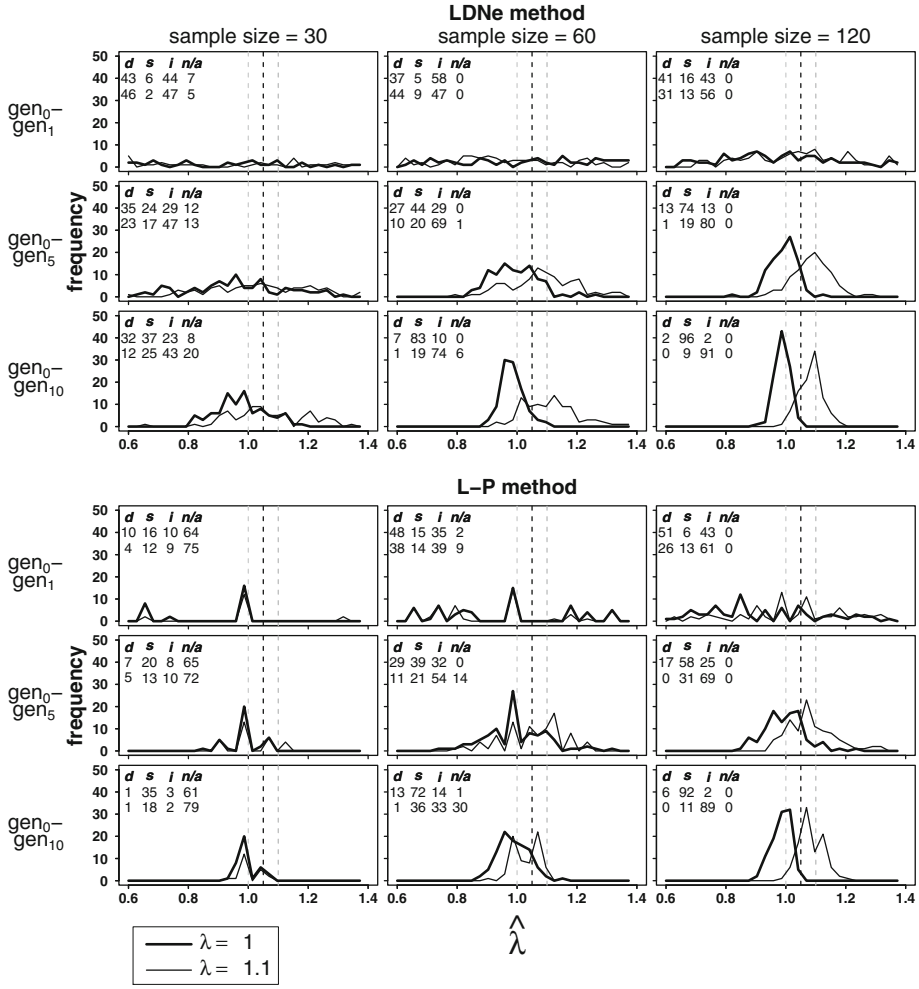

Fig. 1 Distributions of LDNe- and LP-based $\hat{\lambda}$ estimates of population growth rate ($\lambda = 1.0$ or 1.1) with initial $N = 250$. The values in the *upper left* of *each panel* are the number of 100 replicates indicating declining (d; $\hat{\lambda} < 0.95$), stable (s; $0.95 < \hat{\lambda} < 1.05$), increasing (i; $\hat{\lambda} > 1.05$), or inestimable (n/a) $\hat{\lambda}$ for stable (*top row*) and recovering (*bottom row*) populations

Table 1 Percentage of times population trend was correctly identified in stable or increasing populations using the LDNe ($\hat{N}_e$) or LP ($\hat{N}$) methods over a range of initial abundances (N), generations (gens), and sample sizes (S)

		Stable population						Increasing population					
		Gens 0–1		Gens 0–5		Gens 0–10		Gens 0–1		Gens 0–5		Gens 0–10	
		$\hat{N}e$	$\hat{N}$	$\hat{N}e$	$\hat{N}$	$\hat{N}e$	$\hat{N}$	$\hat{N}e$	$\hat{N}$	$\hat{N}e$	$\hat{N}$	$\hat{N}e$	$\hat{N}$
$N = 100$	$S = 30$	50	55	66	50	**83**	67	59	33	**74**	33	**73**	15
	$S = 60$	55	61	**82**	**83**	**98**	**96**	44	48	**77**	68	**90**	**70**
$N = 250$	$S = 30$	49	26	59	27	69	36	47	9	47	10	43	2
	$S = 60$	42	63	**71**	68	**90**	**86**	47	39	69	54	**74**	33
	$S = 120$	57	57	**87**	**75**	**98**	**98**	56	61	**80**	69	**91**	**89**
$N = 500$	$S = 30$	43	10	44	9	50	14	37	1	33	1	33	0
	$S = 60$	51	50	65	56	**75**	55	53	25	54	20	49	7
	$S = 120$	58	58	**81**	**83**	**92**	**93**	47	49	**73**	62	**74**	66
$N = 1000$	$S = 30$	24	2	27	0	40	4	28	1	20	0	18	0
	$S = 60$	33	27	41	26	54	34	38	7	35	6	36	0
	$S = 120$	59	68	64	**71**	**80**	**77**	57	42	54	44	61	38

Values $\geq$70 are in bold text to ease identification

number of individuals available for sampling may not fall within the range of utility of the LDNe method.

N_e estimates may be more useful in real-world populations than the W–F populations simulated here. In W–F populations N and N_e are the same. In cases where high variance in mating success or offspring survival produce small N_e/N ratios, tracking population trends with $\hat{N}_e$ can take advantage of the relatively large effects of genetic drift and make $\hat{N}_e$ a useful index of population trend. For example, if true $N = 1{,}000$, a small N_e/N ratio may make $N_e = 100$ and the population will be subject to large genetic drift and behave genetically like a small population. However, a potential downside to using $\hat{N}_e$ as an index of N is that there may be temporal fluctuations in N_e/N due to changes in the relative reproductive success of individuals. Further investigation of the feasibility of tracking N with $\hat{N}_e$ in recovering populations is warranted, as researchers often can obtain both N with $\hat{N}_e$ estimates from a single dataset if studies are designed carefully.

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