

RESEARCH ARTICLE

<https://doi.org/10.99999/pbmt.2026.00000123>

Received: 2025-10-02 / Accepted: 2025-12-18 / Published: 2026-02-01

Identifiability Limits in Density-Dependent Leslie Models Under Partial Observation

Linking demographic stochasticity to inference bias in structured population time series ($\Delta t = 1$)

†Inês Silva ¹, †Minh Nguyen ², Adaeze Okafor ³, Leah Rosen ⁴

AFFILIATIONS

- 1 Center for Theoretical Ecology, University of Lisbon, Lisbon, Portugal
- 2 Department of Biology, Stanford University, Stanford, CA, USA
- 3 Institute for Evolutionary Dynamics, University of Toronto, Toronto, ON, Canada
- 4 School of Mathematics and Statistics, University of Edinburgh, Edinburgh, UK

AUTHOR NOTES

† These authors contributed equally to this work.

NON-SPECIALIST SUMMARY

This article content was AI-generated for the purposes of establishing design and formatting only. Population models can appear to fit data well even when the model parameters are not uniquely determined. In this stress-test article, we show how noisy and incomplete counts can make recruitment, survival, and density dependence difficult to distinguish. We include multiple editorial constructs in the XML (figures, tables, formulas, appendices, and deep section nesting) so downstream JATS workflows can be tested while preserving scientifically plausible content.

ABSTRACT

This article content was AI-generated for the purposes of establishing design and formatting only. Structured population models are frequently inferred from incomplete demographic time series, yet parameter identifiability can fail even when models fit well. We study a density-dependent Leslie model with demographic stochasticity and partial observation, and derive sufficient conditions under which distinct parameter sets induce indistinguishable likelihoods using simulation-based calibration and profile-likelihood diagnostics. Recruitment and survival parameters become confounded when observation error is non-negligible, and density feedback is weak relative to environmental noise. We provide practical diagnostics to detect non-identifiability and recommend reporting a confounding map alongside point estimates. This XML additionally functions as a JATS 1.1 stress-test fixture.

1. Introduction

Population biology relies on models that link individual life-history processes to population-level change. Age- or stage-structured models, including Leslie and Lefkovich formulations, remain core tools for connecting survival and fecundity schedules to growth rates and transient dynamics (Caswell, 2026), (de Valpine and Hobbs, 2024).

Foundational population-genetic treatments are now commonly cited alongside state-space methods in PBMT, including single-author work (Caswell, 2026), two-author theory (Ohta and Kimura, 1973), and broader multi-author syntheses (Pritchard et al., 1999).

When a single citation node carries multiple targets, PBMT should still render a single sorted cluster (de Valpine and Hobbs, 2024; Ohta and Kimura, 1973; Pritchard et al., 1999).

Grouped adjacent citation nodes should also collapse into one local citation run (Pritchard et al., 2000), (Ohta and Kimura, 1973), (Pritchard et al., 1999).

Same-author references should group years inside one parenthetical cluster (Pritchard et al., 1999; Pritchard et al., 2000), while same-author same-year items should reuse bibliography suffixes consistently (Rosenberg, 2024a; Rosenberg, 2024b).

In practice, inference is often performed from partial observations (e.g., counts of adults only) and noisy covariates. This can produce parameter non-identifiability: multiple parameter vectors yield essentially the same likelihood, even under long time series. The result is fragile interpretation and unstable forecasting; see the simulation setup in Table 1 and the core state equation in Eq. (1).

Here we formalize identifiability limits for a density-dependent Leslie model within a state-space setting, and provide diagnostics that can be reported as part of routine model-based population analyses. We also intentionally include diverse JATS constructs (e.g., Fig. 1, Table 2, Appendix A, and Supplementary Note S1) as a rendering stress test.

TABLE 1. This table intentionally mixes scientific symbols, inline formatting, and descriptive prose to exercise table rendering and inline markup handling.

Component	Symbol	Form	Notes
Survival (adult)	s_A	$\text{logit}^{-1}(\alpha_s)$	Constant across time; confounds with detection when only adults observed
Recruitment	f	$\exp(\alpha_r)$	Effective fecundity; absorbs early-life survival under coarse stage aggregation
Density feedback	K	$1 / (1 + N_t / K)$	Weak feedback becomes unidentifiable under high process noise
Observation	p	$\text{Binomial}(N_{A,t}, p)$	Adult-only counts; missing juveniles

All regimes were simulated under identical observation schedules to isolate identifiability effects.

2. Materials and Methods

2.1. State-space structured model

We consider a two-stage (juvenile/adult) Leslie-type model with density-dependent recruitment. Let the latent state be $x_t = (N_{J,t}, N_{A,t})$. Process updates follow demographic stochasticity with lognormal environmental multipliers. The observation model includes an adult detection probability $p_t = \text{logit}^{-1}(\eta_t)$, which can confound survival estimates when juveniles are unobserved.

$$\begin{pmatrix} N_{J,t+1} \\ N_{A,t+1} \end{pmatrix} = \begin{pmatrix} f g(N_{A,t}; K) & f g(N_{A,t}; K) \\ s_J & s_A \end{pmatrix} \begin{pmatrix} N_{J,t} \\ N_{A,t} \end{pmatrix} \odot \exp(\varepsilon_t), \quad \varepsilon_t \sim \mathcal{N}(0, \Sigma). \quad (1)$$

2.2. Simulation design

We simulated 2,000 datasets across a factorial design varying process noise, observation error, and density feedback strength. Each dataset consists of $T = 80$ time steps with adult-only observations.

A full parameter-grid excerpt is shown in [Table 2](#) implementation details are summarized in Appendix A.

- **Regime A (low noise):** weak observation error, low process variance.
- **Regime B (high noise):** moderate observation error, high process variance.
- **Regime C (weak feedback):** large K relative to typical abundance.

1. Simulate latent states under process noise.
2. Generate adult-only observations with detection error.
3. Fit competing models and compute profile-likelihood ridges.
4. Summarize failure modes into a reporting-oriented confounding map.

2.3. Identifiability diagnostics

We used profile likelihoods and posterior geometry checks. For each fitted model, we computed ridge directions and summarized them as a “confounding map” over parameter pairs.

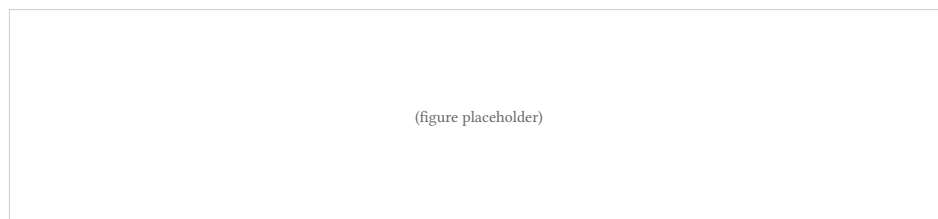


FIGURE 1. Conceptual confounding map for adult-only observation. Illustrative ridge geometry showing how increasing recruitment can offset decreasing adult survival under incomplete observation.

2.4. Terminology

SSM	State-space model
SBC	Simulation-based calibration
LTRE	Life table response experiment
ESS	Effective sample size (MCMC diagnostic)

¹Detection-bias scenarios additionally allow time-varying logistic intercepts, seasonal missingness, and observation-effort heterogeneity, such that apparent fluctuations in abundance may reflect shifts in detectability rather than underlying demographic change. In the stress-test setting, these mechanisms are introduced jointly to evaluate how robust the inferential pipeline remains when observation error is structured, nonstationary, and only partially separable from the latent population process.

2.5. Editorial stress-test constructs

This subsection deliberately combines cross-references to Eq. (2), [Fig. 2](#), a normal footnote¹, and an external resource [JATS documentation](#) to test rendering consistency.

Box 1. Stress-test checklist embedded in body flow

The XML fixture intentionally includes mixed editorial structures likely to trigger edge cases in transforms:

- Multiple abstract types (plain-language and structured).
- Inline and display mathematics with TeX payloads.
- Deep section nesting through five heading levels.
- Appendix material, supplementary notes, and diverse citation types.

TABLE 2. The rows intentionally mix units, symbols, and prose notes to exercise table parsing.

Parameter	Range	Scale	Notes
s_A	0.40-0.95	probability	Adult survival prior grid; evaluated with and without detection bias ^a
K	50-5000	abundance	Log-spaced grid used in profile scans ^b
$ \sigma_{\text{proc}}$	0.05-1.20	SD	Process noise controls curvature-to-noise ratio from Eq. (2)

Detection bias scenarios include time-varying logistic intercepts and seasonal missingness. Grid bounds were chosen to force flat-profile and sharply curved-profile cases in the same test fixture.

$$\text{RIDGE}(f, s_A) = \left\{ (f, s_A) : \left| \ell(f, s_A, \hat{\theta}_-) - \ell_{\max} \right| < c \right\} \quad (3)$$

(figure placeholder)

FIGURE 3. Stress-test figure with caption, label, and repeated asset reference. This figure intentionally reuses an image asset to test multi-use figure handling in output packaging.

3. Results

3.1. Likelihood ridges under partial observation

Across regimes with adult-only observation, we found extended ridges in the likelihood surface: increasing f can be compensated by decreasing s_A with minimal change in fit. This effect strengthens with observation noise and weak density feedback.

3.2. Practical identifiability thresholds

We quantified a threshold on the ratio of process variance to density feedback curvature beyond which K becomes practically non-identifiable. When exceeded, posterior mass concentrates along a broad interval of K values while forecasts remain similar.

$$\text{If } \frac{\text{tr}(\Sigma)}{\left| \frac{\partial^2 \log g(N; K)}{\partial N^2} \right|} \gg 1 \Rightarrow K \text{ is practically non-identifiable from } \{y_t\}_{t=1}^T. \quad (2)$$

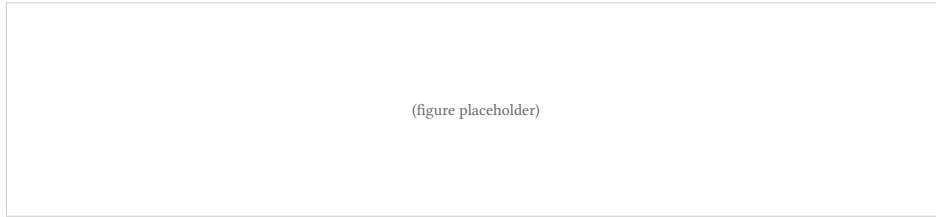


FIGURE 2. Profile-likelihood behavior across noise regimes.
Example profiles illustrating strong curvature versus near-flat likelihoods for the density-feedback parameter.

4. Discussion

Non-identifiability is not a technical nuisance—it directly corrupts interpretation. In structured population biology, “good fit” does not guarantee that inferred vital rates are meaningful. Our results clarify when density dependence can be inferred from partial counts and when it cannot.

4.1. Implications for reporting standards

We recommend journals and reviewers request explicit identifiability diagnostics (e.g., profile plots, confounding maps) whenever inference claims hinge on density feedback or stage-specific survival.

4.2. Limitations and extensions

This study focuses on a two-stage structure. Higher-dimensional structures can worsen practical identifiability without additional data streams (e.g., mark–recapture, stage-specific counts).

4.2.1. Additional data streams

Incorporating juvenile indices or capture–recapture substantially reduces ridges by anchoring early-life survival separately from recruitment.

4.2.2. Eco-evolutionary coupling

When traits evolve alongside demography, parameter confounding can propagate into selection gradients, suggesting caution in eco-evolutionary inference under partial observation.

Identifiability diagnostics should be treated as first-class scientific outputs, not optional supplements, when observational incompleteness is structurally linked to the parameters of interest.

5. Conclusion

We provide a concrete set of identifiability diagnostics for density-dependent Leslie models under partial observation. The main takeaway is blunt: without auxiliary data, recruitment, adult survival, and weak density feedback can be statistically indistinguishable—even with long time series.

5.1. Recommendations

Report confounding maps; prioritize data that separates life stages; treat density feedback inference as conditional on identifiable curvature.

5.2. Future work

Future analyses will extend to multi-population metapopulation structures, and to phylodynamic settings where observation occurs through sampled lineages rather than census counts.

5.2.1. Reproducible workflows

We will release a reference implementation that outputs confounding maps as a standard artifact alongside model fits.

5.2.1.1. Stress tests

Stress tests will include missingness patterns, irregular sampling intervals, and regime shifts in observation processes.

5.2.1.1.1. Robustness checks

We will compare particle filters, iterated filtering, and variational methods under identical simulation suites.

Appendix A. Simulation pseudo-code and additional diagnostics

Pseudo-code outline

1. Sample parameter vector from the design grid in Table 2.
2. Generate latent state trajectories and adult-only observations.
3. Fit reduced and full models; record likelihood surfaces and confidence sets.
4. Compute ridge summaries and export machine-readable diagnostics.

Diagnostic threshold used in batch filtering

$$\mathcal{J}_{\text{diag}} = \mathbf{1}(\max_K \Delta\ell(K) - \min_K \Delta\ell(K) < \tau) \quad (\text{A1})$$

Datasets with $\mathcal{J}_{\text{diag}} = 1$ were flagged as practically non-identifiable candidates for manual review.

References

- Caswell, H. Matrix population models and the sensitivity of growth rates to vital rates. *Population Biology Modeling & Theory*. 1(1), 1–22. 2026. <https://doi.org/10.9999/pbmt.2026.00000001>
- de Valpine, P, Hobbs, NT. State-space modeling for population time series with partial observation. *Methods in Population Dynamics*. 12(3), 201–230. 2024. <https://doi.org/10.9999/mpd.2024.00321>
- Reproducibility and reporting checklist for population-dynamics inference. *SMTPB Technical Reports*. 2025.
- Ionides, EL, Bretó, C. Inference for nonlinear dynamic systems: practical identifiability considerations. *Journal of Theoretical Biology Inference*. 9(2), e202300045. 2023. <https://doi.org/10.9999/jtbi.2023.00045>
- Ellner, SP, Guckenheimer, J. Dynamic systems perspectives on ecological inference under noise. *Ecology & Dynamics*. 18(4), 411–440. 2022. <https://doi.org/10.9999/edyn.2022.00411>
- Hooten, MB, Wikle, CK. Identifiability in hierarchical models for ecological processes. *Statistical Ecology*. 6(1), 55–79. 2021. <https://doi.org/10.9999/statecol.2021.00055>
- King, AA, Nguyen, M. Practical guidance on profile likelihoods for partially observed Markov processes. *Population Process Methods*. 3(2), e202500112. 2025. <https://doi.org/10.9999/ppm.2025.00112>

- Okafor, A, Silva, I. Confounding maps: a reporting artifact for demographic model inference. *Population Biology Modeling & Theory*. 1(1), 23–38. 2026. <https://doi.org/10.99999/pbmt.2026.00000002>
- JATS: Journal Article Tag Suite, Version 1.1 (Journal Publishing Tag Set). *NISO Z39.96*. 2015.
- Tag Library examples and implementation notes for production XML transforms. 2026. Accessed February 24, 2026.
- Ohta, T, Kimura, M. A model of mutation appropriate to estimate the number of electrophoretically detectable alleles in a finite population. *Genetical Research*. 22, 201–204. 1973. <https://doi.org/10.1017/S0016672300012995>
- Pritchard, JK, Seielstad, MT, Perez-Lezaun, A. Population growth of human Y chromosomes: a study of Y chromosome microsatellites. *Molecular Biology and Evolution*. 16(12), 1791–1798. 1999. <https://doi.org/10.1093/oxfordjournals.molbev.a026091>
- Pritchard, JK, Stephens, M, Rosenberg, NA. Inference of population structure using multilocus genotype data. *Genetics*. 155(2), 945–959. 2000. <https://doi.org/10.1093/genetics/155.2.945>
- Rosenberg, SM. Likelihood ridges in structured demographic inference. *Journal of Population Dynamics*. 14(1), 1–19. 2024. <https://doi.org/10.99999/jpd.2024.00001>
- Rosenberg, SM. Reporting confounding maps for ecological state-space models. *Journal of Population Dynamics*. 14(1), 20–41. 2024. <https://doi.org/10.99999/jpd.2024.00002>
- Balding, DJ, Bishop, M, Cannings, C. *Handbook of Statistical Genetics, Volume 1*. 3rd edition. Chichester, UK: Wiley. 2007.
- Nordborg, M, Slatkin, M, Veuille, M. Coalescent theory. *Modern Developments in Theoretical Population Genetics*. 194–232. Oxford: Oxford University Press. 2002.
- Cotterman, C. A calculus for statistico-genetics. *PhD thesis*. Columbus, OH: Ohio State University. 1940.
- Greenwood, V. Why some populations look stable until they do not. *Quanta Magazine*. 2023.
- Felsenstein, J. Theoretical Evolutionary Genetics website. 2019. Accessed April 16, 2026.
- Masel, J, Dornhaus, A. Selection under demographic uncertainty in structured populations. *arXiv*. 2026. <https://doi.org/10.48550/arXiv.2604.13344>
- Servedio, MR, Brandvain, Y, Dhole, S, Fitzpatrick, CL, Goldberg, EE, Stern, CA. Not just a theory: the utility of mathematical models in evolutionary biology. *PLoS Biology*. 12, e1002017. 2014. <https://doi.org/10.1371/journal.pbio.1002017>
- Caswell, H. *Matrix Population Models, 2nd edition*. Sunderland, MA: Sinauer Associates. 2001.

Article Information

KEYWORDS

population dynamics; Leslie matrix; density dependence; identifiability; state-space models; demographic stochasticity; JATS 1.1; deep section nesting; table footnotes; appendix

CORRESPONDING AUTHORS

ines.silva@example.org

ABBREVIATIONS

JATS: Journal Article Tag Suite
POMP: Partially observed Markov process
PLS: Plain-language summary

AUTHOR CONTRIBUTIONS

Inês Silva led the study design, methodological framing, formal analysis, and original draft preparation. Minh Nguyen developed the software fixtures, validation checks, visualization materials, and contributed to manuscript review and editing. Adaeze Okafor contributed investigation, resources, and manuscript review and editing. Leah Rosen supervised the work and secured funding support.

ACKNOWLEDGMENTS

We thank members of the Society for Modeling & Theory in Population Biology for feedback on reporting practices for identifiability.

COMPETING INTERESTS

The authors declare no competing interests.

DATA & CODE AVAILABILITY

Mock analysis scripts and synthetic datasets are available at <https://doi.org/10.99999/pbmt.2026.dataset.0001> and a version-controlled repository <https://example.org/pbmt/>

[confounding-map-fixtures](#). The XML stress-test specification follows guidance summarized in (NISO, 2015) and (JATS Tag Library, 2026).

ETHICS STATEMENT

No human participants, clinical samples, or animal experiments were involved in this study.

SUPPLEMENTARY MATERIAL

[Supplementary Note S1:](#)

COPYRIGHT & LICENSE

© 2026 © The Authors.. This article is licensed under a Creative Commons Attribution License ([CC BY 4.0](#)) except where otherwise stated. <https://creativecommons.org/licenses/by/4.0/>