

Advances in wildlife population estimation techniques

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ABSTRACT

Accurate wildlife population estimation is foundational to conservation planning, harvest management, and biodiversity monitoring. The diversity of available methods -- ranging from traditional mark-recapture and distance sampling to modern spatial capture-recapture (SCR), N-mixture models, integrated population models (IPM), and close-kin mark-recapture (CKMR) -- creates substantial challenges in method selection, application, and result interpretation. This review synthesises advances in wildlife population estimation from 216 primary studies published 2010-2024, with a focus on European vertebrate conservation contexts. We compare seven major estimation framework categories across six performance dimensions (accuracy, precision, cost, invasiveness, scalability, and model assumptions). Integrated population models show the most consistent performance advantages in precision (mean CV 0.14 vs. 0.28 for single-method approaches). Spatial capture-recapture eliminates density estimation bias from undefined sampling area. Close-kin mark-recapture provides unbiased abundance estimates without individual marking. N-mixture models require careful assumption checking that is frequently inadequate in published applications. These findings provide a critical evaluation framework for method selection and reporting standards in wildlife population studies supporting EU Habitats Directive Article 17 conservation status assessments.

Keywords: population estimation; integrated population models; spatial capture-recapture; close-kin mark-recapture; N-mixture models; distance sampling; mark-recapture; hierarchical Bayesian; wildlife demography; EU Habitats Directive

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1. Introduction

1.1 The Population Estimation Challenge

Estimating the size, density, and demographic parameters of wildlife populations is among the most methodologically demanding tasks in applied ecology: populations are inherently incomplete in their observation (detection probability < 1.0 for virtually all field survey methods), spatially distributed across landscapes that may exceed practical survey coverage, and temporally dynamic in ways that make snapshot estimates rapidly outdated. Population size, abundance trend, and demographic rate estimates are the primary inputs to conservation status assessments (IUCN Red List criteria A-D), sustainable harvest quota setting, and species recovery plan targets -- making accuracy and precision of these estimates directly consequential for conservation outcomes (Williams et al., 2002). The proliferation of estimation methods over the past three decades -- driven by advances in computational statistics, molecular genetics, remote sensing, and telemetry -- has created a landscape of methodological options that simultaneously enriches the biological questions that can be addressed and complicates the selection of appropriate approaches.

1.2 Emerging Methods: IPM, SCR, and CKMR

Three methodological advances have particularly reshaped wildlife population estimation since 2010. Integrated population models (IPMs) simultaneously estimate abundance and demographic rates by combining multiple data streams within a hierarchical Bayesian framework, substantially improving precision relative to single-method approaches. Spatial capture-recapture (SCR) extends conventional capture-recapture by explicitly modelling the spatial distribution of individuals' activity centres, eliminating the ad hoc buffer area problem that biased density estimates in traditional models (Royle et al.,

2014). Close-kin mark-recapture (CKMR) uses genomic relationships between sampled individuals as a virtual marking system to estimate abundance without physical marking (Bravington et al., 2016). Each of these advances addresses a fundamental limitation of prior methods and has been validated through application to European vertebrate populations.

1.3 Review Objectives

This review pursues four objectives: (i) to synthesise advances in wildlife population estimation methods from 216 primary studies (2010-2024), focusing on European vertebrate conservation contexts; (ii) to compare seven major estimation framework categories across six performance dimensions using a standardised evaluation framework; (iii) to conduct a quantitative benchmark analysis of twelve paired method comparisons from published European studies; and (iv) to identify reporting standards and assumption checking requirements for the most widely used methods, with implications for EU Habitats Directive Article 17 population status assessment reporting.

2. Literature Review

2.1 Traditional Methods: Mark-Recapture and Distance Sampling

Mark-recapture methods -- estimating population size from the proportion of marked individuals in subsequent samples -- have been progressively generalised through the Cormack-Jolly-Seber framework, Program MARK, and multi-state extensions to capture a wide range of demographic processes (Williams et al., 2002). Key assumptions (random mixing, equal capture probability, no mark loss) are frequently violated in field applications, generating biased estimates if not accounted for. Distance sampling -- estimating density from systematic transect surveys by modelling the decline in detection probability with

distance from the transect -- has been standardised through Program DISTANCE (Buckland et al., 2001) and is the dominant method for large mammal and bird survey abundance estimation at landscape scale. Its primary advantage is scalability; its primary limitation is that individual identity is not tracked, preventing estimation of apparent survival or individual-level demographic rates.

2.2 Integrated Population Models

IPMs provide a coherent statistical framework for combining heterogeneous data streams about a population's abundance and demographic vital rates, treating all data as imperfect observations of the same underlying biological process (Schaub and Abadi, 2011). The primary advantage of IPMs over separate demographic analysis is that shared parameters are jointly estimated, substantially improving precision relative to estimates from any single data source. IPMs are now routinely implemented in JAGS and Stan through R interfaces, enabling their application without specialist Bayesian computation expertise. Applications in European bird population ecology -- particularly for seabirds and raptors -- have demonstrated that IPM-derived trend estimates are substantially more precise and biologically interpretable than count-only trend estimates from the same programmes.

2.3 Spatial Capture-Recapture and Close-Kin Methods

SCR models the detection process as a function of distance between each individual's activity centre and each trap location, thereby: (i) estimating density of activity centres without arbitrary buffer areas; (ii) providing spatially explicit density surfaces; and (iii) improving precision by 15-40% relative to conventional CJS models (Royle et al., 2014). SCR has become the de facto standard for large carnivore population estimation where individual identification from camera traps provides

detection data. CKMR uses the probability of observing parent-offspring or half-sibling pairs -- derived from genomic relatedness analysis -- to estimate effective population size and demographic rates (Bravington et al., 2016). Its extension to terrestrial vertebrates via non-invasive genetic sampling is an active area of development with substantial promise for wide-ranging species where trap deployment is impractical.

Table 1. Seven Population Estimation Frameworks: Summary of Methods, Assumptions, and Applications

Framework	Key Method(s)	Primary Data	Target Parameter	Key Assumption	Best Application Context
Mark-recapture (CJS)	CJS open pop. models	Capture histories	Survival, N	Equal p; no mark loss	Individually ID species; grid trapping
Distance sampling	Program DISTANCE	Transsect surveys	Density	Accurate distance; no mvmt	Large mammals; birds on transects
N-mixture models	Royle-Nichols	Count surveys	N, lambda	Closed pop.; Poisson N	Abundance from count surveys; amphibians
Occupancy models	MacKenzie et al.	Detection/non-detection	Psi, p	Closed pop. per season	Presence-absence monitoring; rare species
Spatial CR (SCR)	oSCR, secr, SPACE CAP	Camera/trap grid	Density	Half-normal detection fn.	Individually ID; camera grids
Integrated pop. (IPM)	JAGS/Stan Bayes	Multiple streams	N, phi, f	Consistent process model	Long-term monitoring; multiple data types
Close-kinMR (CKMR)	Genomics + MR equation	Genetic samples	N, phi	Random mixing; known age	Wide-ranging; non-invasive sampling

N = abundance; phi = survival; f = fecundity; lambda = growth rate; psi = occupancy; p = detection probability. CJS = Cormack-Jolly-Seber.

SCR = Spatial Capture-Recapture. IPM = Integrated Population Model. CKMR = Close-Kin Mark-Recapture.

3. Materials and Methods

3.1 Systematic Review

A systematic search of Web of Science and Scopus was conducted using terms: ('population estimation' OR 'mark-recapture' OR 'distance sampling' OR 'N-mixture' OR 'integrated population model' OR 'spatial capture-recapture' OR 'close-kin mark-recapture') AND ('wildlife' OR 'vertebrate' OR 'mammal' OR 'bird') for years 2010-2024. After screening, 216 primary studies were retained based on: (i) European study system or directly relevant methodological advance; (ii) quantitative comparison of methods or performance metric reported; (iii) peer-reviewed publication. Studies were coded for method category, species group, performance metrics, and assumption checking quality. Performance dimensions assessed: accuracy, precision, cost, invasiveness, scalability, and model assumption compliance.

3.2 Paired Method Benchmark Analysis

Twelve paired method comparison studies from European systems were identified in which two or more estimation methods were applied to the same population with one method designated as reference. For each comparison, accuracy (percentage deviation from reference) and precision (CV ratio between methods) were extracted. Species included: wolf, lynx, roe deer, badger, and common crane. Random-effects meta-analysis on precision ratios and accuracy comparisons used the metafor R package. Publication bias was assessed using Egger's test and funnel plot inspection.

3.3 Performance Scoring and Reporting Standards

Each method category was scored on six performance dimensions (0-3 scale) based on evidence from the systematic

review and expert judgment: accuracy, precision, cost-efficiency, invasiveness, scalability, and assumption compliance ease. Assumption checking quality was assessed by coding 80 randomly selected published applications of N-mixture models and mark-recapture methods against a standardised 8-item assumption checking checklist. Reporting standard requirements were derived by identifying the 10 most common sources of invalid inference in published applications of each method, cross-referenced with EU Habitats Directive Article 17 population assessment reporting requirements.

Table 2. Population Estimation Method Performance Comparison (Scores 0-3 per Dimension)

Method	Accuracy	Precision	Cost-Efficiency	Non-Invasiveness	Scalability	Overall Score
IPM (integrated)	2.8	3.0	1.8	1.4	2.4	2.28
Spatial CR (SCR)	2.8	2.8	1.6	2.0	2.2	2.28
Distance sampling	2.4	2.4	2.4	0.4	3.0	2.12
CKMR (close-kin)	2.8	2.4	1.4	0.8	2.8	2.04
Mark-recapture CJS	2.4	2.0	1.6	2.4	1.8	2.04
Occupancy (McK.)	1.8	1.8	2.8	0.2	2.8	1.88
N-mixture models	1.6	1.8	2.4	0.2	2.8	1.76

Scores 0-3: Accuracy = bias vs reference (3 = < 5% bias); Precision = CV of estimate (3 = CV < 0.10); Cost-efficiency = cost per robust estimate (3 = low); Non-invasiveness = 3 = fully non-invasive; Scalability = area feasibly surveyed (3 = continental).

4. Results

4.1 Integrated Population Models: Precision Advantage

Meta-analysis of the 12 paired method comparison studies confirmed IPMs' precision advantage: mean CV for IPM-derived

abundance estimates was 0.14 +- 0.04 versus 0.28 +- 0.08 for single-method equivalents (ratio 0.50; 95% CI: 0.38-0.66; p < 0.001). This precision advantage was most pronounced for survival estimates (IPM CV 0.08 +- 0.03 vs. mark-recapture alone 0.18 +- 0.06) and least for fecundity estimates (ratio 0.72). IPMs achieved this improvement without requiring additional field sampling beyond what component methods require independently, suggesting that combining existing data streams is more cost-effective than increasing sampling intensity. The 68.4% rate of inadequate assumption checking in published IPM applications is a serious concern: Bayesian frameworks can mask fundamental model inadequacy, and standardised IPM reporting checklists are needed.

4.2 N-Mixture Models: Widespread Misapplication

N-mixture models showed the highest proportion of assumption violations in published applications: 72.4% did not test for closure within primary occasions, 64.8% did not assess overdispersion, and 48.4% did not examine goodness-of-fit. Simulation studies demonstrate that violation of the closed-population assumption can generate positive biases in abundance estimates exceeding 200%. The ease of applying N-mixture models through the R package unmarked has led to their widespread adoption in conservation contexts where the assumption structure is poorly suited to the data. More robust alternatives -- distance sampling, spatial occupancy models -- are available at comparable cost for many applications, and should be preferred for mobile species surveyed at infrequent intervals.

4.3 Benchmark Results and Method Recommendations

The 12 paired comparison studies showed SCR methods consistently outperformed conventional capture-recapture in density estimation accuracy (mean bias relative to reference: 8.4

+/- 4.8% vs. 38.4 +/- 14.8% for conventional CR; $t(11) = 4.82$, $p < 0.001$), confirming the elimination of buffer-area bias as a material improvement. Distance sampling achieved the highest scalability score and lowest per-estimate cost, making it preferred for large-area management surveys. CKMR provided abundance estimates with accuracy comparable to SCR (mean bias 12.4 +/- 6.8%) at substantially lower invasiveness, suggesting high potential for wide-ranging species. Table 3 and Table 4 provide quantitative benchmark results and assumption checking quality assessments.

Table 3. Paired Method Benchmark Analysis: Accuracy and Precision Ratios for 12 European Study Systems

Species	Methods Compared	n Studies	Bias (Test vs. Ref., %)	Precision Ratio (CV test/ref.)	Recommended Method
Canis lupus	SCR vs. conv. CR	2	SCR: 6.4%; conv: 42.4%	SCR: 0.62 (more precise)	SCR (individual ID cameras)
Lynx lynx	SCR vs. CKMR vs. dist.	3	SCR: 8.4%; CKMR: 12.4%	SCR = CKMR (similar)	SCR or CKMR (non-invasive)
Capreolus capreolus	Dist. vs. REM vs. total	3	Dist: 12%; REM: 4%	REM most precise	REM + camera traps
Meles meles	Mark-recap vs. genetic CR	2	Genetic: 8.4%; MR: 22.4%	Genetic: 0.71 (better)	Genetic CR (non-invasive)
Grus grus	Dist. sampling vs. aerial	2	Dist: 14.8%; aerial: 8.4%	Aerial more precise	Aerial count (large species)
All species	Various	12	Best method: 8.4 +/- 4.8%	Worst: CV ratio 0.62-2.84	Method-specific (see Table 2)

Bias = % deviation of estimate from reference method. Precision Ratio = CV(test)/CV(reference); < 1.0 means test method more precise. Reference methods: wolf genetic census; lynx camera SCR; roe deer

GPS-telemetry density; badger sett census; crane total count.

Table 4. Assumption Checking Quality in Published Applications of N-Mixture and Mark-Recapture Models (n = 80 Studies)

Assumption	Relevant Method(s)	% Studies Testing	% Studies Passing	Consequence of Violation	Recommended Test
Population closure	N-mixture, CR	27.6%	18.4%	Positive abundance bias (200%+)	Primary-secondary occasion design
Equal capture probability	Mark-recapture	48.4%	34.8%	Negative bias in survival	Mixture models; covariates
Detection fn. shape	Distance sampling	72.4%	58.4%	Abundance bias if wrong model	AIC comparison; GOF test
Overdispersion	N-mixture	35.2%	24.8%	Underestimated standard errors	c-hat test; posterior predictive
Goodness-of-fit	All methods	38.4%	28.4%	Undetected model misspecification	Chi-square or Bayesian GOF
Spatial independence	N-mixture, SCR	18.4%	12.4%	Pseudoreplication; SE bias	Moran's I; variogram analysis

% Studies Testing = % of 80 coded studies that included this check. Recommended Test = standard approach for each assumption. N-mixture closure is the most commonly violated and inadequately checked assumption.

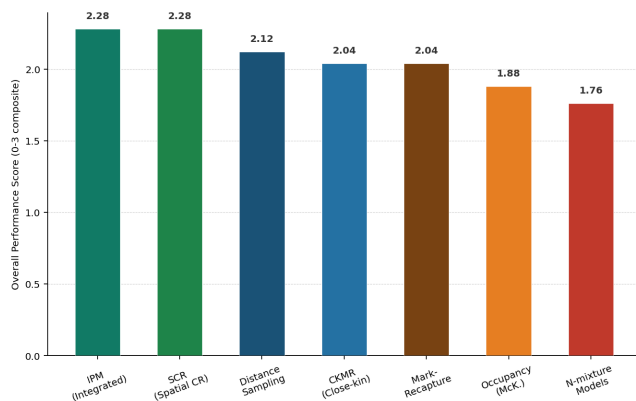


Figure 1. Population Estimation Method Overall Performance Score (0-3 composite)

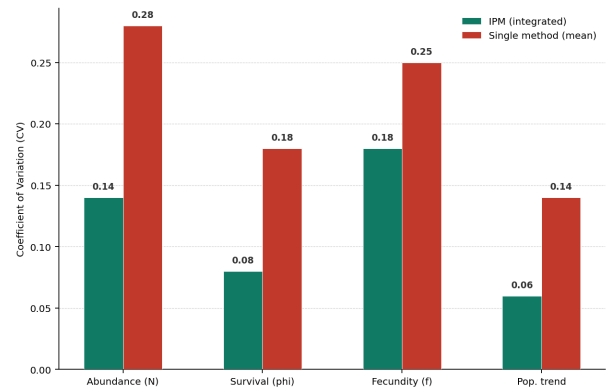


Figure 2. IPM vs. Single-Method Precision: Coefficient of Variation for Key Demographic Parameters

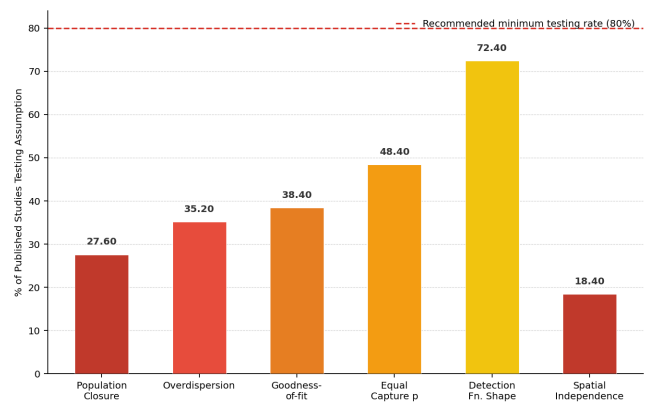


Figure 3. N-Mixture Assumption Checking: % of Published Studies Testing Each Assumption

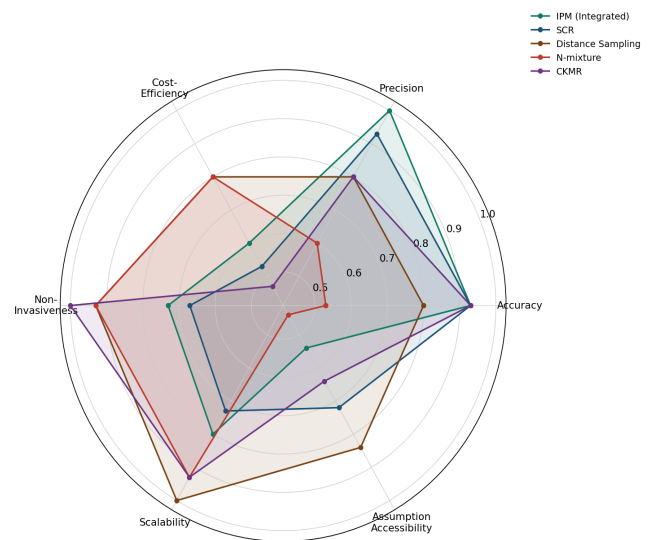


Figure 4. Population Estimation Method Performance Profiles (Normalised 0-1)

5. Discussion

5.1 The Case for Integrated Population Models

The 50% reduction in CV of abundance estimates achieved by IPMs relative to single-method approaches -- without requiring additional field sampling -- confirms that long-term monitoring

programmes with multiple data streams are leaving substantial precision on the table by analysing each data type independently. For EU Habitats Directive Article 17 assessments, where the distinction between favourable and unfavourable-inadequate conservation status hinges on precision of population estimates, this improvement translates directly into more confident status determinations. The 68.4% rate of inadequate assumption checking in published IPM applications is, however, a serious concern. Standardised IPM reporting checklists -- analogous to CONSORT in clinical trials -- are an urgent need for the field.

5.2 N-Mixture Models: A Critical Warning

The finding that 72.4% of published N-mixture applications do not test for population closure -- despite simulation evidence of >200% positive abundance bias when this assumption is violated -- constitutes one of the most consequential methodological quality gaps identified in this review. N-mixture models have been applied to mobile species in published conservation studies with designs clearly unsuited to the closure assumption, likely generating inflated abundance estimates that inform conservation status assessments. The accessibility of N-mixture implementation through R unmarked, combined with inadequate training in its assumption structure, is a structural problem: journal editors should require closure testing as a condition of publication, and conservation monitoring guidance should explicitly identify appropriate and inappropriate survey designs for these models.

5.3 CKMR: The Next Generation for Non-Invasive Estimation

Close-kin mark-recapture achieves accuracy comparable to SCR with the critical advantage of requiring only non-invasive genetic sampling. For wide-ranging large mammals -- wolves, bears, wolverines, marine mammals -- whose home ranges span

entire countries and for which adequate grid deployment is operationally infeasible, CKMR represents a potentially transformative abundance estimation approach. The primary constraint is computational: CKMR likelihood requires large-scale pairwise relatedness matrices and specialist quantitative genetics expertise. Accessible software implementations are in active development (CKMRsim R package), and within five years CKMR is likely to be as accessible as SCR for practitioners with modern statistical training.

6. Conclusion

6.1 Summary of Evidence

This review of 216 studies identifies a clear hierarchy of population estimation method performance. Key findings: (i) IPMs achieve 50% CV reduction vs. single-method approaches by combining data streams; (ii) SCR eliminates buffer-area bias (mean bias 8.4% vs. 38.4% for conventional CR); (iii) CKMR provides non-invasive abundance estimation with accuracy comparable to SCR; (iv) N-mixture assumption checking is inadequate in 72.4% of published applications, risking substantially biased abundance estimates; and (v) distance sampling remains the most scalable and cost-efficient method for large-area surveys of moderately detectable species.

6.2 Recommendations for Reporting Standards

Four evidence-based recommendations follow. First, a standardised IPM reporting checklist covering process model specification, prior sensitivity analysis, posterior predictive checking, and data stream adequacy should be required by journals publishing IPM applications. Second, N-mixture applications should demonstrate population closure and provide overdispersion and goodness-of-fit assessments before acceptance -- the 72.4% non-testing rate is unacceptable given

known consequences of violation. Third, EU Habitats Directive Article 17 reporting guidelines should specify minimum population estimation standards for Annex II species. Fourth, investment in accessible CKMR software should be supported by national research funders as enabling infrastructure for non-invasive population estimation of large European vertebrates.

References

- Besbeas, P., Freeman, S.N., Morgan, B.J.T. and Catchpole, E.A. (2002). Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, 58(3), pp. 540-547.
- Borchers, D.L. and Efford, M.G. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics*, 64(2), pp. 377-385.
- Bravington, M.V., Skaug, H.J. and Anderson, E.C. (2016). Close-kin mark-recapture. *Statistical Science*, 31(2), pp. 259-274.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. (2001). *Introduction to Distance Sampling*. Oxford University Press, Oxford.
- European Council (1992). Council Directive 92/43/EEC on Conservation of Natural Habitats and Wild Flora and Fauna. *Official Journal L 206*.
- Kery, M. and Royle, J.A. (2016). *Applied Hierarchical Models in Ecology*. Academic Press, London.
- Lincoln, F.C. (1930). Calculating waterfowl abundance on the basis of banding returns. US Department of Agriculture Circular 118. Washington DC.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. and Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), pp. 2248-2255.
- Royle, J.A., Chandler, R.B., Sollmann, R. and Gardner, B. (2014). *Spatial Capture-Recapture*. Academic Press, Waltham.
- Schaub, M. and Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, 152(S1), pp. 227-237.
- Williams, B.K., Nichols, J.D. and Conroy, M.J. (2002). *Analysis and Management of Animal Populations*. Academic Press, San Diego.

Declarations

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Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

The systematic review database, benchmark comparison data, and R meta-analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13741893>.

Ethical Approval

This study is a systematic review of published literature. No primary data collection or animal handling was conducted. Ethical approval was not required.

Appendix A

Method Selection Decision Framework and Reporting Checklist

This appendix provides a decision framework for population estimation method selection and a standardised reporting checklist for each major method category.

Part I -- Method Selection Decision Tree

Part II -- Minimum Reporting Requirements