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Quantifying risk of overharvest when implementation is uncertain

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Abstract

1. Sustainable harvest management implies an ability to control harvest rates. This is challenging in systems that have limited control of resources and resource users, which is often the case in small game harvest management. The difference between management strategies and actual harvest bag size (i.e. implementation uncertainty) may be substantial, but few studies have explored this.
2. We investigated how different management strategies and ecosystem variables affected realised harvest of willow ptarmigan (*Lagopus lagopus* L.) among nine independently managed, state-owned hunting areas in Central and South Norway during 2008–2015. First, we focused our empirical analysis around three response variables of interest: hunting bag (scaled by area), hunting effort (number of hunting days scaled by area) and hunter efficiency (shot birds per hunting day). Akaike information criteria (AIC) guided model selection among candidate GLMMs. Then, we used model-averaged parameter estimating from the statistical models in numerical simulations to explore risk of overharvest due to implementation uncertainty.
3. The most parsimonious model explaining hunting bag included total allowable catch (TAC) and willow ptarmigan density. Hunting effort was explained by number of permits sold and type of quota (daily vs. weekly quota). The most parsimonious model describing hunter efficiency only included the effect of willow ptarmigan density.
4. Our results show that managers have only partial control over harvest rates in this system, and that hunters were relatively more efficient and harvest rates higher at low densities. This effect was present for all management strategy scenarios, including when managers adjusted TAC according to population estimates from monitoring programmes.
5. *Synthesis and applications*. Quantifying risk of unsustainable harvest rates under different scenarios enables managers to make informed decisions, when dealing with competing objectives of harvest opportunities and sustainability. The substantial risk of high harvest rates at low densities reported here should encourage frequent use of threshold strategies. This study is one of the first approaches for quantifying implementation uncertainty in small game harvest, and shows how estimates from empirical analyses could be used to quantify risk of overharvest.

KEYWORDS
grouse, harvest rates, hunter efficiency, hunting effort, implementation uncertainty, management strategy, scenarios, small game, sustainable exploitation, willow ptarmigan

1 | INTRODUCTION

Research into the difference between management strategies and actual harvest bag, commonly termed “implementation uncertainty” (Christensen, 1997) or “partial controllability” (sensu Williams, 2001), is rare in terrestrial systems (Milner-Gulland et al., 2010). To date, most studies investigating the link between management decisions and harvest rates do not address the issue of implementation uncertainty, although imperfect information often leads to a gap between implemented regulations and desired outcome (Deroba & Bence, 2008). Furthermore, studies of implementation uncertainty have often focused on to what extent resource users comply with control rules (Bunnefeld, Hoshino, & Milner-Gulland, 2011), but other forms of implementation uncertainty may be of greater concern in many systems. For example, in management of large carnivores, an important aspect of implementation uncertainty is when hunters fail to obtain the set quota, hence management targets of removal are not met (Bischof et al., 2012). In the case of recreational small game harvest, the objective is often to avoid overexploitation while still providing hunting opportunities to the public. Implementation of harvest regulations is often unpredictable in small game harvest systems, such as for greater sage-grouse *Centrocercus urophasianus* (Connelly, Reese, Garton, & Commons-Kemner, 2003), greater prairie-chicken *Tympanuchus cupido* (Powell, Taylor, Lusk, & Matthews, 2011) or waterfowl (U.S. Fish and Wildlife Service, 2016).

A framework that has proven to be particularly useful (e.g. Edwards, Bunnefeld, Balme, & Milner-Gulland, 2014) when there are multiple uncertainties associated with elements in the management cycle is management strategy evaluation (MSE). Management strategy evaluation enables comparison of alternative management strategies using numerical simulations, while incorporating lack of accurate knowledge (Milner-Gulland & Shea, 2017; Milner-Gulland et al., 2010). Here we investigate an essential part of the MSE framework—the path between management decisions and actual harvest, and explore how implementation uncertainty affects the managers’ potential to control offtake. We use willow ptarmigan (*Lagopus lagopus* L.) as a model species for exploring the drivers of small game harvest rates. Willow ptarmigan is a medium-sized tetraonid (Pedersen & Karlsen, 2007). Harvest of the species is a highly relevant topic at a Fennoscandian scale, resulting from a >10-year decrease in abundance throughout the area (Kålås, Husby, Nilsen, & Vang, 2014; Lehikoinen, Green, Husby, Kålås, & Lindström, 2014). It was recently listed as near threatened (NT) in the Norwegian Red List of Species (Henriksen & Hilmo, 2015). Globally willow ptarmigan is listed as least concern (LC), but decreasing population trends have been reported, especially in Europe (BirdLife International 2016). As high harvest mortality is mostly additive to natural mortality (found by Pedersen et al., 2004; Sandercock, Nilsen, Brøseth, & Pedersen, 2011 for a 30% harvest mortality), an important conservation issue is to understand how management strategies affect actual harvest offtake. The objectives of this study were to explore this connection by:

1. Empirical evaluation of the role of management strategies and natural ecosystem parameters (not under management control) on observed harvest bag records, using data from state-owned land in Norway where several common harvest strategies for willow ptarmigan are applied. As management strategies and ecosystem parameters may affect harvest bags indirectly, through either increased hunting effort or higher hunter efficiency, we used two complementary approaches for our analyses to widen our understanding of the system.
2. Modelling implementation uncertainty by quantifying risk of exploitation above specific harvesting thresholds, under different harvest decision scenarios and population states, with estimates from the empirical evaluations. The actual harvest decision scenarios are chosen from the empirical data, and we aim to identify applied constant and proportional management strategies.

This study shows a method for including implementation uncertainty in a management strategy evaluation (MSE), by quantifying risks of high harvest rates under different management strategies and game densities.

2 | MATERIALS AND METHODS

2.1 | Study area and period

The study area consists of management units (MUs) that independently manage state-owned land in Central and South Norway (locally termed “fjellstyrer”). These are required by law to provide hunting opportunities to the public (https://lovdata.no/lov/1975-06-06-31), while still ensuring sustainable harvest management (https://lovdata.no/lov/2009-06-19-100). In the context of this study, we collected data from MUs that registered population estimates of willow ptarmigan through a common web portal (Hønsefuglportalen, http://honsefugl.nina.no; Nilsen, Pedersen, & Vang, 2013). From a total of 23 MUs that are currently using this common e-infrastructure, 16 provided data on management decisions and harvest bags for this study. From these 16 MUs, 10 MUs provided data on all variables central for our analyses. One of the 10 MUs was excluded from analyses because there were only data from a single year. In total, 43 observations across nine MUs from 2008 to 2015 were used as a basis for our analyses. Spatial distribution and number of observations in different years are reported in Figure S1.

Because the majority of the birds are shot early in the hunting season (Kastdalen, 1992; supported by raw data in this study), we based our analyses on data from the first weeks of the hunting season. MUs usually implement stronger restrictions and collect more precise harvest data in the first period of the harvest season, usually lasting ca. 3 weeks. Harvest was performed as walked-up hunting with shotguns, with or without use of pointing dogs. Most MUs include areas that are not suitable for willow ptarmigan (e.g. forested lowlands or high alpine areas; Pedersen & Karlsen, 2007). We thus adjusted the area of each MU to reflect habitat relevant for willow ptarmigan better (see Appendix S1).

2.2 | Harvest and management strategy data

Harvest bag statistics and information about variables expected to have an impact on harvest bags were collected from all MUs having access to such information (cf. Table 1 for a complete overview of variables, and Appendix S1 for additional information about the method). Not all hunters reported back to the managers after their hunt, but managers keep control of hunting reports on an individual (i.e. hunting permit) basis. To estimate total number of hunting days and harvest bags, respectively, we divided the reported numbers for each year and MU by the reporting rate (i.e. proportion of hunters that reported their hunt: mean across years and MUs 71%, range: 37%–100%) for the given MU in a given year. In addition to management decisions that were reported directly by the MUs, i.e. number of purchased permits, season start, type of quota (daily bag limit, periodic bag limit, combination of both) and season length, we also estimated the composite variable TAC (defined as total allowable catch per km^2). Total allowable catch (TAC) incorporates the two main strategies managers apply to restrict harvest: restricting effort and restricting bag size. For periodic quotas, TAC = number of permits sold × quota size, while for daily quotas, TAC = number of hunting days in permits sold × quota size. For the combination quotas, TAC was calculated similarly to period quotas, as this represented the maximum possible catch in these two cases.

2.3 | Ecosystem data

Estimates of population density for each MU each year for willow ptarmigan were based on line transect data, with field procedures following distance sampling methods (Thomas et al., 2010). In August each year, volunteer personnel used trained pointing dogs to search both sides of the transect line, and recorded cluster size (i.e. ptarmigan covey size) and perpendicular distances to observed birds. This procedure has been shown to be a suitable technique, respecting the assumptions of the distance sampling method (Pedersen, Steen, Kastdalen, Svendsen, & Brøseth, 1999; see also Appendix S1). The total dataset (n = 3,020 observations) was analysed in R version 3.2.3 (R Core Team, 2015) using function “ds” in package “Distance” (Miller, 2015). To estimate number of chicks per female willow ptarmigan, we made the assumption that the sex ratio in the populations is equal and that all broods are accompanied by two adults. This last assumption was made to reduce potential biases caused by wrongly classifying juveniles as adults (E.B. Nilsen, pers. com). Based on these data, number of chicks per female (hereafter “production”) was estimated using generalised linear models (GLMs) assuming a binomial error structure, following the procedure outlined in Kvasnes, Pedersen, Storaas, and Nilsen (2014).

TABLE 1 Parameters used to explore the relationship between harvest, management strategies and ecosystem characteristics

Parameter	Excl. from model[a]	Description (unit)
Responses		
Harvest bag	2a, 2b	Number of bagged birds per km^2 suitable habitat, scaled by hunter response rate
Hunting effort (also predictor)	2b	Number of hunting days per km^2 suitable habitat, scaled by hunter response rate
Hunter efficiency	1, 2a	Number of bagged birds per hunting day, scaled by hunter response rate
Predictors: management decisions		
Permits sold	2b	Number of permits sold per km^2 suitable habitat
Length of prime season	2b	Number of days hunters are distributed on
Season start		Categorical: (1) Season opening 10 September , or (2) postponed (i.e. 5–10 days later)
Quota type		Categorical: (1) Day quota, (2) period quota or (3) a combination of the two
TAC (total allowable catch per km^2)		Function of (1) number of hunting days in permits sold × daily quota, or (2) number of permits sold × period quota, both per km^2 suitable habitat
Predictors: ecosystem characteristics		
Willow ptarmigan density		Number of birds per km^2
Willow ptarmigan production		Number of chicks per female, assuming equal sex ratio and brood sizes >2
Habitat structure	2a	Proportion of highland birch forest in suitable terrain
Precipitation		Daily average precipitation (mm) for available hunting days in each area
Temperature		Daily average temperature (°C) for available hunting days in each area

[a]“Exclusion from model” indicates parameters not included in analyses for a given model.

It has previously been reported that hunting efficiency is lower in dense (i.e. forested) habitats compared to open habitats (Pedersen et al., 1999). To address this finding, we calculated the proportion of birch forest within suitable willow ptarmigan habitat for each MU (Appendix S1) and included this as an index for hunting efficiency in the models.

Weather conditions may also affect hunting effort, performance of hunters or dogs, or behaviour and/or habitat use by the game species. Based on data from The Norwegian Meteorological Institute (publicly available from http://eklima.met.no), we used weather variables measured locally, as recommended by Frederiksen, Lebreton, Pradel, Choquet, and Gimenez (2014). We chose the closest weather stations providing daily registrations of precipitation (mean 2.2 stations, range 1–3) and temperature (mean 1.2 stations, range 1–2), using the arithmetic average of the stations for each MU and year. A total of 21 stations with a mean distance of 8.2 km (range 3.2–21.7) from the MU borders were used.

2.4 | Empirical evaluation

We used two separate paths for analysing observed harvest related to management strategies and ecosystem parameters (Figure 1); one where we analysed harvest bag (defined as bagged birds per km^2) as response (model 1), and another where we analysed harvest as a function of hunting effort (model 2a) and hunter efficiency (model 2b). Defining hunting effort as hunting days per km^2 and hunter efficiency as bagged birds per hunting day (commonly known as catch-per-unit-effort, CPUE), we used the relationship hunting days per km^2 × bagged birds per hunting day = bagged birds per km^2 to explore alternative paths to actual harvest rates.

Initial inspection of residuals indicated temporal (year) and spatial (MU) dependencies when fitting the full model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Thus, to account for pseudoreplication, we opted to use mixed models (Zuur et al., 2009), fitting random intercepts for MUs and year (package "lme4", Bates, Mächler, Bolker, & Walker, 2015). When using models that accounted for this dependency, no further temporal (ACF; autocorrelation function) or spatial (Moran's I; package "lctools", Kalogirou, 2016) autocorrelation was evident. Response variables were based on count data and thus assumed to follow Poisson or negative binomial distributions. After constructing generalised linear mixed effects models (GLMMs) assuming the data followed a Poisson distribution, assessment of model residuals from the full models revealed overdispersion for all response variables. Thus, we used negative binomial mixed models (Zuur et al., 2009) to model effects of predictors conditional on group characteristics. Because the size of areas (models 1 and 2a) and time (model 2b) differed, we used the scale parameter (area or time) as an offset, following the recommendation by e.g. Zuur et al. (2009).

To avoid overparameterisation (given a total sample size n = 43), we restricted the set of candidate models to include models with ≤3 fixed effects, in addition to the random intercepts (see above). The variables TAC and hunting effort (when used as a predictor) are directly affected by the other management decisions, thus they are not included simultaneously with other management variables in any model. Some predictors were correlated and thus are not included simultaneously in models to avoid affecting parameter estimates (Zuur, Ieno, & Elphick, 2010), including density with production, season starting time with temperature and season length, and number of permits sold with habitat structure. A Pearson correlation of 0.6 (Graham, 2003) between continuous predictors was used as a collinearity threshold. For categorical variables, correlated predictors were identified through boxplots. All models not including correlated variable pairs were included in the model set. The most parsimonious models were selected using Akaike information criterion (Akaike, 1973) corrected for small sample sizes (AIC$_c$; package "AICcmodavg", Mazerolle, 2016). Model fit was examined by inspecting residuals vs. fitted values and confirming

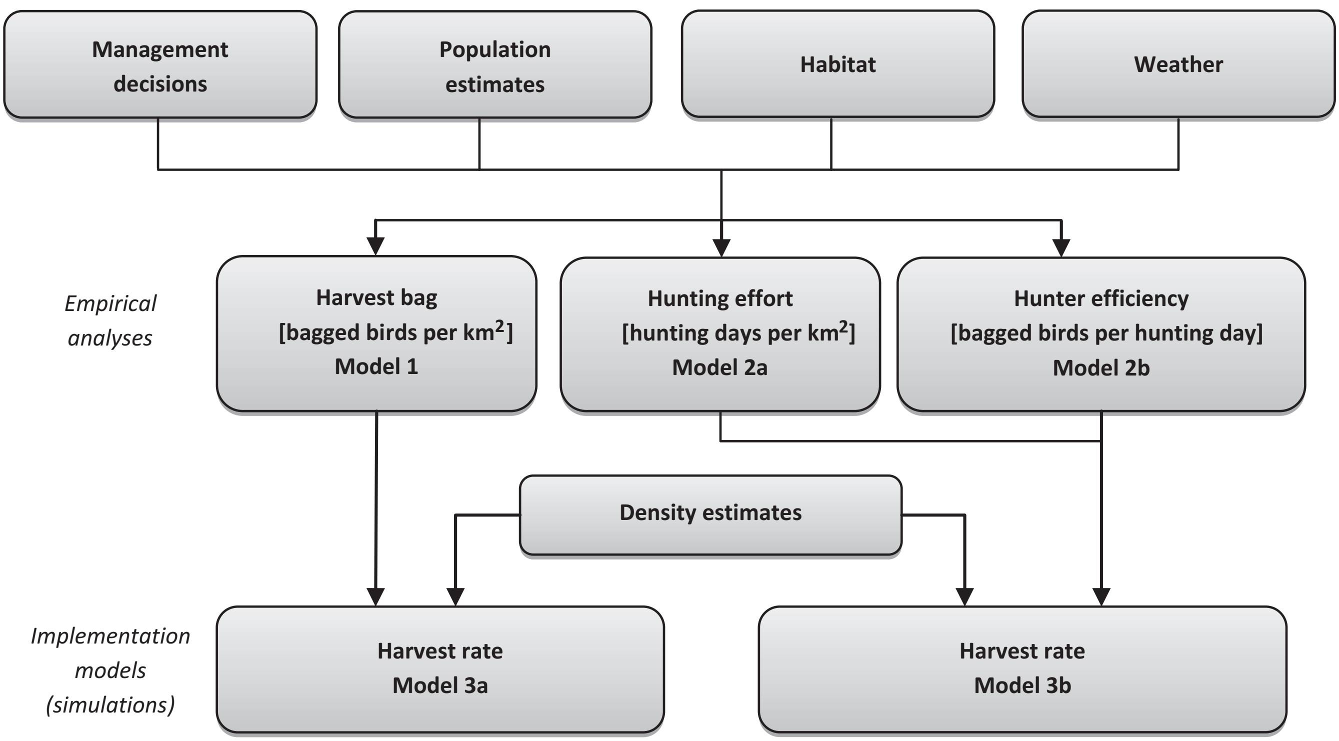

FIGURE 1 Schematic structure of predictors (top line) used for empirical analyses, and the two alternative paths for applying the estimates with standard errors from the results in implementation model simulations

normal distribution of random effects. Furthermore, we performed model-averaging (Grueber, Nakagawa, Laws, & Jamieson, 2011) to give weighted estimates and relative importance of all predictor variables. Models were averaged over the set of models within 95% confidence of cumulative AIC_c weight, using the "zero method" where parameter estimates and standard errors are set to zero when absent in a model (Burnham & Anderson, 2002). To obtain model-averaged estimates for the levels of categorical variables (that might not be present in all models in the candidate set), we first used the sum-contrast in the original model-averaging procedure. Then, we used the delta method (package "car", Fox & Weisberg, 2011) to obtain proper estimates of level-based intercepts. Continuous variables were centred on their means to facilitate interpretation.

To identify whether different willow ptarmigan densities lead to a response in management decisions, we performed a Spearman correlation test on density vs. the management decisions with highest relative importance, on subsets of all MUs. A positive correlation value above 0.5 was used as a criterion for a more than random positive relationship between the parameters. The two groups (proportional and constant strategy) were analysed separately to reveal strength of the relationship with density (as input for the simulated strategies), using linear models with Gaussian error distribution.

2.5 | Simulating harvest rates

Partly based on the statistical analyses described above, we performed numerical simulations to assess effects of implementation uncertainty on realised harvest rates and risk of overharvest. Following the logic governing the statistical models, we used two structurally different pathways between collected data and implementation models (Figure 1) and modelled a range of scenarios. The endpoints of our

TABLE 2 AIC_c model selection tables. Top models within cumulative weight = 0.95 and null models from empirical analyses, where (1) models harvest bag, (2a) hunting effort and (2b) hunter efficiency. Full AIC_c model selection tables are available in Table S2

Model	Par	AIC_c	ΔAIC_c	AIC_c weight
(1)				
Density + TAC	6	541.92	0.00	0.29
Density + TAC + temperature	7	542.08	0.15	0.27
Density + TAC + precipitation	7	542.12	0.20	0.26
Density + TAC + habitat	7	544.73	2.81	0.07
Density + quota type + temperature	8	545.65	3.73	0.04
Null	4	594.91	52.99	0.00
(2a)				
Permits sold + quota type + temperature	8	548.29	0.00	0.49
Permits sold + quota type + density	8	550.05	1.76	0.20
Permits sold + quota type + production	8	550.89	2.60	0.13
Permits sold + quota type + precipitation	8	552.30	4.01	0.07
Permits sold + quota type + season start	8	552.85	4.56	0.05
Null	4	615.73	67.44	0.00
(2b)				
Density	5	556.41	0.00	0.27
Density + habitat	6	558.33	1.92	0.10
Density + TAC	6	558.39	1.98	0.10
Density + precipitation	6	558.79	2.38	0.08
Density + season start	6	558.91	2.50	0.08
Density + temperature	6	559.01	2.60	0.07
Density + TAC + habitat	7	560.17	3.75	0.04
Density + habitat + precipitation	7	560.75	4.34	0.03
Density + TAC + precipitation	7	560.77	4.36	0.03
Density + quota type	7	560.96	4.55	0.03
Density + TAC + temperature	7	561.06	4.65	0.03
Density + habitat + temperature	7	561.17	4.76	0.03
Season start + density + habitat	7	561.18	4.77	0.03
Season start + density + precipitation	7	561.23	4.82	0.02
Null	4	582.80	26.39	0.00

TAC, total allowable catch per km^2.

TABLE 3 Model-averaged parameter estimates and relative importance of parameters based on AIC_c weights of all models within cumulative weight = 0.95, where non-present parameters are given the value zero. Categorical parameters are compared to overall mean instead of to one factor level and continuous parameters are centred on their means

Parameter	Relative importance	Model-averaged estimate ± *SE* (log)
(1)		
(Intercept)		0.180 ± 0.159
Density	1.00	0.031 ± 0.007
TAC	0.95	0.058 ± 0.014
Temperature	0.33	0.017 ± 0.032
Precipitation	0.28	0.009 ± 0.017
Habitat	0.08	−0.069 ± 1.040
Quota type (1)	0.05[a]	0.018 ± 0.083
Quota type (2)	0.05[a]	0.006 ± 0.036
(2a)		
(Intercept)		0.594 ± 0.067
Quota type (1)	1.00[a]	0.205 ± 0.049
Quota type (2)	1.00[a]	0.030 ± 0.085
Permits sold	1.00	1.140 ± 0.144
Temperature	0.52	0.022 ± 0.024
Density	0.22	0.003 ± 0.005
Production	0.14	0.008 ± 0.021
Precipitation	0.07	0.002 ± 0.009
Season start (1)	0.05	0.005 ± 0.023
(2b)		
(Intercept)		−0.507 ± 0.133
Density	1.00	0.055 ± 0.008
Habitat	0.24	−0.683 ± 1.924
TAC	0.21	0.002 ± 0.005
Precipitation	0.18	−0.003 ± 0.012
Season start (1)	0.13	0.006 ± 0.042
Temperature	0.13	0.001 ± 0.011
Quota type (1)	0.03[a]	0.002 ± 0.019
Quota type (2)	0.03[a]	−0.003 ± 0.028

TAC, total allowable catch per km^2.
[a]Categorical parameters get one value for all levels.

simulations were harvest rates emerging from different harvest decisions and state variables. Importantly, we were here not modelling the impact of different harvest rates on the population state dynamics. In general, our simulation model consisted of four submodels that were linked in the following way:

1. Population state model: First, we generated a true value for the population density (willow ptarmigan per km^2) in time t, by taking random draws from a uniform distribution between 2 and 25 (covering the range of densities in our dataset). This state variable (X_t) was the input variable for the observation model, but its value will not be known to the managers (see below).
2. Observation model: Based on the true population density (X_t), we simulated a system where managers are monitoring the population state. In our simulations, we assumed that the managers had access to unbiased density estimates and that the precision resembled the precision in the distance sampling density estimates reported here. Across all years and areas, the median coefficient of variation (CV) was estimated at 0.23. The observation model thus generated random draws (D_t) based on a Gaussian distribution with mean = X_t and standard deviation = CV × X_t. The estimated density emerging from the observation model (D_t) is the input for the harvest decision model, and will be available to managers in contrast to the true state (X_t).
3. Management decision model: Based on the information available to them, the managers make decisions about harvest regulations. Following our statistical analysis and the range of the empirical data, we identified five relevant scenarios corresponding to model 3a (Figure 1) and six to model 3b.
4. Implementation model: The management decisions affect realised harvest rate following the relationships revealed by the statistical models. For each scenario, we simulated harvest rates under the range of true population states, where model-averaged estimates and standard errors from the empirical analyses were used to replicate model uncertainty. Only estimates of parameters with substantial relative importance were included, using a threshold of 0.8 as guidance for suggesting high importance, while the remaining parameters were kept at their means. All simulations were replicated 10,000 times.

We were not interested in exploring the effects of harvest rates on willow ptarmigan demography and population dynamics. To illustrate how our approach could be extended to assess this feedback, being part of a full MSE model (Figure S2), we replaced the random number generator (see point 1 above) with a population model including feedback from the system (see Figure S3 for a simple example), and simulated the process across 100 time steps.

Sandercock et al. (2011) found that harvest of 15% of the population was at least partially compensated by a decrease in natural mortality, while 30% harvest lead to super-additive mortality in study areas in Norway. We apply these two harvest rate levels in the context of our study and here define “overharvest” as the excess of these levels. The quantitative output from our simulations was thus used to estimate the risk of exploitation above harvest rates of 15% and 30% for the management strategies tested, given the uncertainties. As a validation for the simulation exercise, different values for uncertainties in the observation model and implementation model were applied to investigate robustness to changes in population estimate precision, and to vulnerability to underestimation of errors in the implementation models.

3 | RESULTS

Initial habitat analyses revealed that on average 70.3% (range 28.3%–92.3%) of the MU areas are suitable habitat for willow ptarmigan,

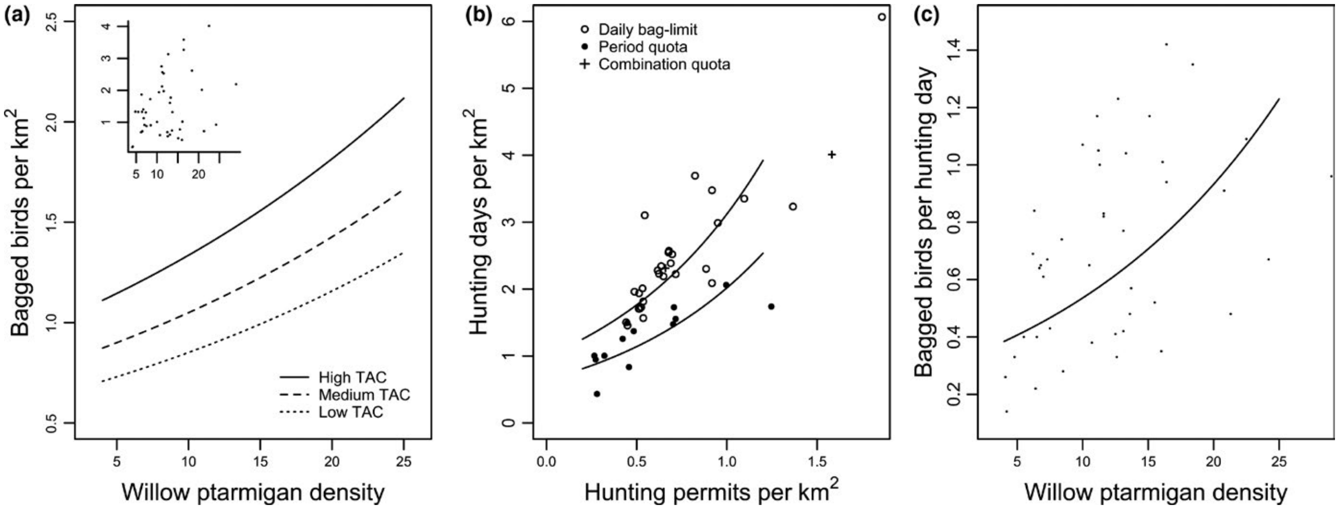

FIGURE 2 Results of empirical analyses, where (a) shows harvest bag (model 1) in relation to willow ptarmigan density and TAC (total allowable catch per km^2). The relationship is plotted with three selected values (first, second and third quartile in the data) of TAC as examples, to visualise harvest bag at various densities, conditional on a level of TAC. Insert in upper left corner shows raw data observations. (b) Displays hunting effort (model 2a) as a function of sold hunting permits per km^2 and quota type. The upper line predicts the hunting effort with daily bag limits, lower line with period quotas. The two observations with quotas that are combinations of the others are not included in the predictions. Hunter efficiency (model 2b) in relation to willow ptarmigan density is shown in (c). For standard errors, cf. Table 3

resulting in an effective size range of the study areas of 113.7 to 1,058.0 km^2 (mean 473.4 km^2). Mean proportion of forested habitat within MU areas was 10.4% (range 2.9–17.2), the rest being bogs, heathland or other open areas. Estimated population densities for willow ptarmigan ranged from 4.1 to 29.0 willow ptarmigan per km^2, with mean density 12.1. Numbers of chicks per female were between 2.0 and 6.1, averaging at 3.5 (mean CV = 14.1%).

3.1 | Empirical analyses

Model selection guided by AIC$_c$ (Table 2 and Table S2) and the model-averaging procedure indicated that the most parsimonious model describing harvest bag (model 1) included TAC and willow ptarmigan density (Table 3). These variables had substantially higher relative importance than other variables. Both TAC and density were positively related to harvest bags, and the combined effects indicate that a low TAC at higher densities gives harvest bags comparable to a high TAC at lower densities (Figure 2a). If TAC is set at a high level (third quartile in this study; TAC = 11.5), harvest bags at five birds per km^2 is 57% higher than if TAC was set at a low level (first quartile; TAC = 3.7).

Both number of permits sold (scaled by km^2) and type of quota were important predictors of hunting effort (Tables 2 and 3; model 2a). In general, daily quotas resulted in higher hunting effort than period quotas, when the number of permits sold was the same (Figure 2b).

Ptarmigan density was the main predictor of hunter efficiency and, based on the most parsimonious model, hunters clearly responded with higher efficiency with increasing density (Table 3). However, the slope of the relationship indicates that hunters were *relatively* more efficient at lower densities, as an increase in density was not met with a proportional increase in catch per hunting day across the range of densities observed here (Figure 2c). Unaveraged parameter estimates from the most parsimonious models are made available for the readers in Table S3, in case they are needed in e.g. meta-analyses.

The Spearman correlation test relating willow ptarmigan density to management decisions from the most parsimonious models identified for model 1 (harvest bag), three MUs in a group that adapted their TAC in relation to density estimates. The selection was confirmed by visual inspection of paired line plots of TAC and density through the years. TAC was modelled as a function of density to reveal how the managers responded to different population states. For the proportional TAC strategy group, the model with density was better than the alternative intercept-only model (ΔAIC$_c$ = 4.62, AIC$_c$ weight = 0.91, slope ± *SE*: 0.624 ± 0.216, r^2 = 0.34). For the other group, the intercept-only model (i.e. a constant TAC disregarding density) best described the management strategy (ΔAIC$_c$ = 2.59, AIC$_c$ weight = 0.79, intercept ± *SE*: 8.917 ± 1.296). There were no indications of groups with proportional versus constant management strategies for the other models (i.e. model 2a describing hunting effort and 2b describing hunter efficiency).

3.2 | Simulations

Implementation uncertainty under the first pathway (model 3a; Figure 1) was explored through simulating harvest rates under five different scenarios: the proportional TAC strategy (with estimates from the model TAC ~ density above) and four representative constant TAC scenarios (TAC equal to 5, 10, 15 and 20, and *SE* standardised to 1.5 for all runs). The proportional strategy had a fairly constant harvest rate along medium and high density values, but this increased notably as densities decreased (Figure 3). At five birds per km^2, although no risk of exceeding the 30% threshold, there was a 49.7% risk of harvest rates above the 15% level (cf. Table 4). A constant TAC of 10, slightly

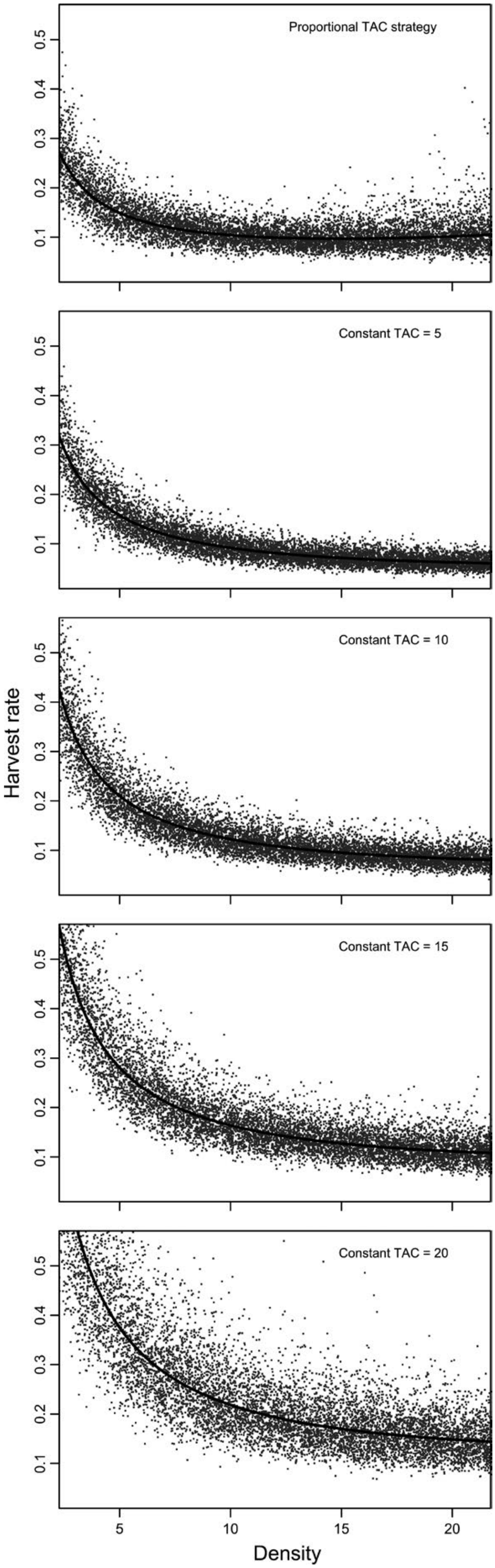

FIGURE 3 Simulations of five TAC strategy scenarios. The plots show harvest rate in relation to willow ptarmigan density under a proportional TAC strategy, where the management adjusts TAC (total allowable catch per km^2) in relation to the observed density, and four constant TAC strategy scenarios. Simulated values (n = 10,000) are shown as grey dots. Black line is the line for the same simulation without uncertainty in any parameters, representing mean values along the x-axis over an infinite number of simulations

above average in the data, showed an 5.1% risk of harvest above at the highest level and 93.9% at the 15% level when density dropped to five birds per km^2.

Under implementation model 3b (Figure 1), we explored harvest rates at different constant effort strategies only, combining the models for hunting effort and hunter efficiency. We selected three representative scenarios of permits sold per km^2 (i.e. 0.5, 0.75 and 1.0) within each of the two main quota types. Daily quotas overall gave higher harvest rates (Figure 4), with a 36.5% risk of harvest above the 15% level at five birds per km^2 and 0.5 permits sold per km^2 (Table 5). Risk rapidly increased with increasing number of permits sold. For period quotas, there was still substantial risk (68.6%) of overshooting the 15% level at lower densities with 1.0 permits sold.

Comparing the performance of the proportional TAC model under assumptions of different uncertainties in the observation model (using the upper and lower 90% interval values, CV = 0.43 and 0.15), demonstrated fairly high robustness to observation uncertainty (Table S4). Assuming increased parameter uncertainties in the implementation models did, as expected, affect the risk of harvest above the tested thresholds, but had little effect on predicted harvest rate means.

4 | DISCUSSION

Resource managers use a number of strategies to avoid excessive harvest of small game populations, such as limiting the number of hunting permits available, setting daily bag limits or shortening the hunting season (Kurki & Putaala, 2010). However, without knowledge about the effect of such control efforts, managers have no real control of harvest offtake even if they implement limitations. The results from our study clearly indicate that both ecosystem parameters, especially willow ptarmigan density, and management procedures are affecting actual harvest. The most parsimonious model for harvest bag (model 1) included both TAC and willow ptarmigan density. As TAC is a function of permits sold and quota size, managers may adjust one or both of these parameters to approach the desired harvest level. However, often a large proportion of permits for small game hunting in this study and elsewhere (e.g. Kurki & Putaala, 2010) is sold before population surveys are obtained. This leaves less flexibility to react to current population states with a change in TAC. Furthermore, even if managers use a proportional TAC strategy, the general trend in the simulations implies that due to implementation uncertainty the risk of overharvest is still present when densities are low. An additional matter to consider is that we used data from the first weeks of the hunting season. Although the

TABLE 4 TAC strategy harvest. Harvest rate means and risks of harvest rates above two specified levels (15% and 30%) for simulated scenarios within the TAC strategies (model 1). Means and risks are presented for three levels of willow ptarmigan density, where the values are calculated over the range ± 1 of the density level (e.g. 4–6 for density 5)

	Density 5 ± 1			Density 10 ± 1			Density 15 ± 1		
TAC strategy	HR mean (*SD*)	RHR >0.15	RHR >0.30	HR mean (*SD*)	RHR >0.15	RHR >0.30	HR mean (*SD*)	RHR >0.15	RHR >0.30
Proportional TAC	0.153 (0.034)	49.7%	0.0%	0.106 (0.020)	2.6%	0.0%	0.100 (0.028)	2.7%	0.0%
Constant TAC = 5	0.163 (0.035)	61.8%	0.1%	0.093 (0.018)	0.7%	0.0%	0.072 (0.014)	0.0%	0.0%
Constant TAC = 10	0.214 (0.047)	93.9%	5.1%	0.125 (0.025)	14.3%	0.0%	0.097 (0.019)	1.5%	0.0%
Constant TAC = 15	0.291 (0.071)	100.0%	38.4%	0.168 (0.036)	68.8%	0.1%	0.131 (0.027)	19.8%	0.0%
Constant TAC = 20	0.393 (0.111)	100.0%	79.2%	0.227 (0.062)	94.5%	11.5%	0.177 (0.047)	69.3%	1.3%

HR, harvest rate; *SD*, standard deviation; RHR, simulated risk of harvest rates above specified levels; TAC, total allowable catch per km^2.

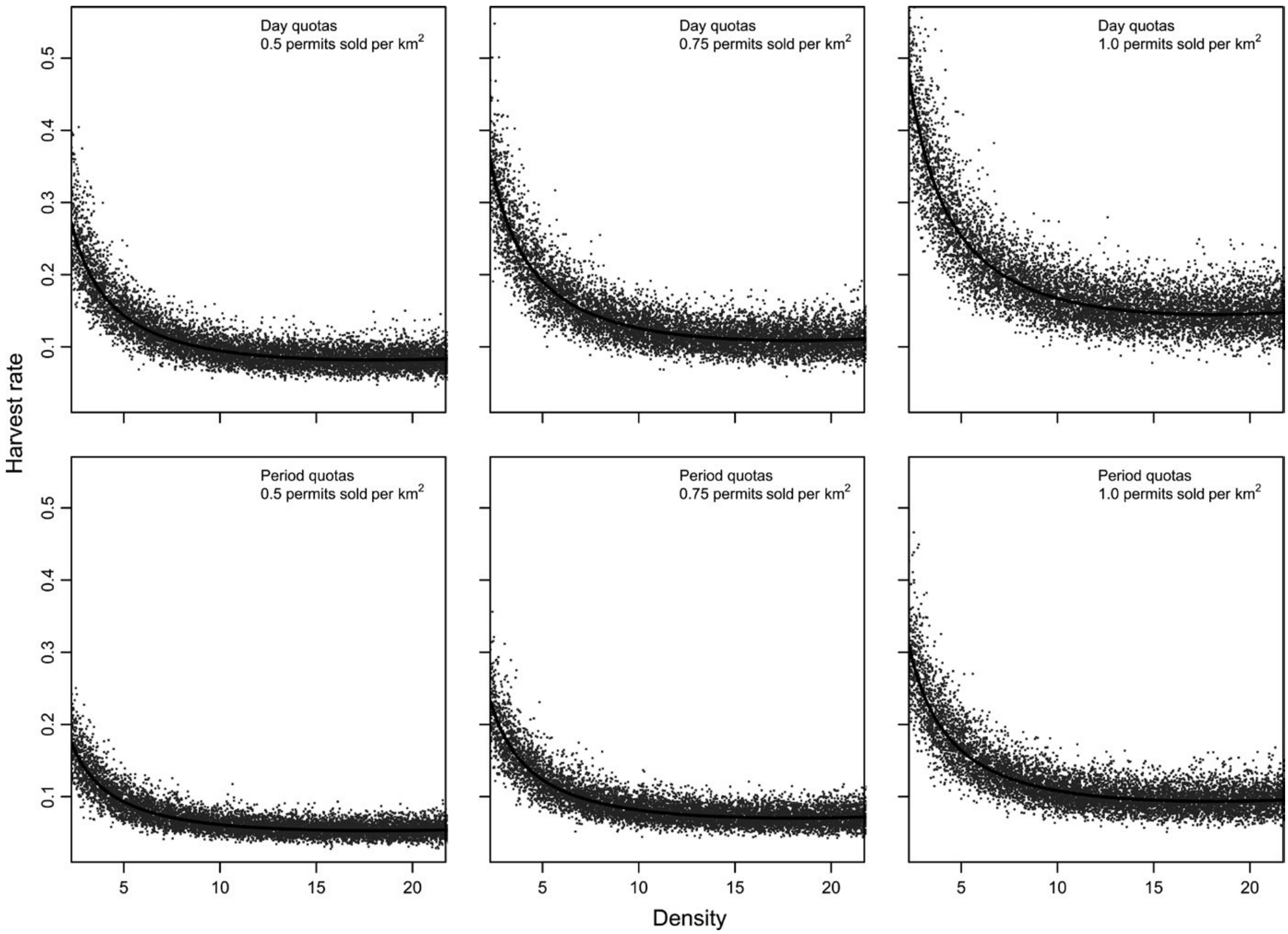

FIGURE 4 Simulations of six effort strategy scenarios. The plots show harvest rate in relation to willow ptarmigan density, given the quota sizes in the study, for day and period quota scenarios with 0.5, 0.75 and 1.0 permits sold per km^2. Simulated values (n = 10,000) are shown as grey dots. Black line is the line for the same simulation without uncertainty in any parameters, representing mean values along the x-axis over an infinite number of simulations

TABLE 5 Effort strategy harvest. Harvest rate means and risks of harvest rates above two specified levels (15 and 30%) for simulated scenarios within the effort strategies (model 2), given the quota sizes in the study. Means and risks are presented for three levels of willow ptarmigan density, where the values are calculated over the range ± 1 of the density level (e.g. 4–6 for density 5)

Effort strategy		Density 5 ± 1			Density 10 ± 1			Density 15 ± 1		
Quota type	Permits per km^2	HR mean (*SD*)	RHR >0.15	RHR >0.30	HR mean (*SD*)	RHR >0.15	RHR >0.30	HR mean (*SD*)	RHR >0.15	RHR >0.30
Day	0.50	0.144 (0.027)	36.5%	0.0%	0.096 (0.015)	0.3%	0.0%	0.084 (0.013)	0.0%	0.0%
	0.75	0.195 (0.036)	90.2%	0.6%	0.128 (0.019)	11.9%	0.0%	0.111 (0.017)	2.5%	0.0%
	1.00	0.261 (0.049)	99.9%	21.4%	0.169 (0.029)	74.5%	0.0%	0.150 (0.026)	47.1%	0.0%
Period	0.50	0.094 (0.019)	0.7%	0.0%	0.062 (0.010)	0.0%	0.0%	0.054 (0.009)	0.0%	0.0%
	0.75	0.126 (0.024)	16.1%	0.0%	0.083 (0.013)	0.1%	0.0%	0.073 (0.012)	0.0%	0.0%
	1.00	0.168 (0.033)	68.6%	0.0%	0.109 (0.018)	2.0%	0.0%	0.097 (0.016)	0.1%	0.0%

HR, harvest rate, *SD*, standard deviation, RHR, simulated risk of harvest rates above specified levels.

majority of hunting occurs in this period, additional harvest throughout the season will increase the harvest rates presented here.

Hunting effort affects total bag size (Caro, Delibes-Mateos, Viñuela, López-Lucero, & Arroyo, 2015; this study), and has thus been used as a control-tool in harvest management. We found that number of permits sold together with quota type best explained hunting effort. While the effect of number of permits sold is intuitive, the additional effect of quota type was not expected. Through the simulation exercise, it is clear that the use of day quotas have a notable effect on harvest rates and the risk of exceeding the defined levels. Although hunting effort could be limited if a hunter filled the period quota before the hunting permit expired, it is a likely assumption that the majority of hunters were unable to fill their quotas (Bischof et al., 2012), regardless of quota type. We suggest that the lower hunting effort associated with period quotas mostly had a behavioural basis, where hunters with period quotas might have expected to fill their quota within the period, thus holding back on the effort to avoid filling it too early. If this suggestion is correct, we believe this behavioural aspect could be useful in harvest management in general, as it would provide a simple but effective tool for managers to lower harvest rates while still providing hunting opportunities.

The modest positive relationship between ptarmigan density and harvest bag (model 1), as well as between density and hunter efficiency (model 2b), is in line with previous studies of both willow ptarmigan and other species (Harley, Myers, & Dunn, 2001; Post et al., 2002; Willebrand, Hörnell-Willebrand, & Asmyhr, 2011). The increased relative efficiency may be explained by hunters compensating for having few encounters by hunting over longer days at low densities (Willebrand et al., 2011), or by the limitation of only being able to fire double-barrelled shotguns twice in each shooting situation regardless of encountered number of animals (Andersen & Kaltenborn, 2013). In addition, if willow ptarmigan select for certain types of microhabitat, hunter efficiency would be expected to remain fairly stable for experienced hunters when densities are reduced. Such density-dependent relative catchability is expected to have detrimental effects on animal populations (Pitcher, 1995). In this context, a fixed-effort strategy, commonly implemented to limit overharvest (Hörnell-Willebrand, 2010), should be used with caution when densities decrease.

Overexploitation of harvested species may lead to continued low abundance (Courchamp, Clutton-Brock, & Grenfell, 1999) and even population extinctions (Sutherland, 2001). Population declines have been linked to lack of controllability in the implementation, and especially in fisheries, the examples are numerous (see e.g. Deroba & Bence, 2008). Constant management strategies are particularly problematic with regard to overexploitation (Fryxell, Packer, McCann, Solberg, & Sæther, 2010). We assume that managers chose a constant TAC model from one out of two reasons. They may expect hunting mortality to be compensatory, thus not considering population state to be important. There is an ongoing debate concerning whether tetraonid hunting mortality is compensatory or additive to natural mortality (see e.g. Sandercock et al., 2011; Sedinger, White, Espinosa, Partee, & Braun, 2010), although there is at any rate likely to be more compensation at high population densities (Péron, 2013). Alternatively, managers trust hunters to reduce harvest bags sufficiently with decreasing game abundances. This study strongly contradicts the latter aspect, as all competing scenarios gave increased harvest rates at lower densities. An implication of this is that even managers with conservative constant strategies face high risk of overharvest when population densities are low, unless they apply extremely precautionary strategies compromising satisfaction for hunters and objectives for managers (Andersen et al., 2008).

4.1 | Management implications

The model developed and presented here, quantifying the ecological risks of harvest levels above the selected thresholds, is applicable for informed trade-off decisions between ecological and societal sustainability. When risk of high harvest rates is substantial, managers defying this risk increase the probability that harvest affects population development negatively (Sandercock et al., 2011). This study shows that in systems where managers do not have direct control over harvest bags, harvest rates typically increase with decreasing density. This can be a common feature of systems where detailed management of both resources and resource users is challenging, such as in small game harvest systems like for red-legged partridge in Spain (Díaz-Fernández, Viñuela, & Arroyo, 2012), for European ducks (Elmberg et al., 2006) or as in recreational fresh water fishing (Allen, Miranda, & Brock, 1998). A consequence is that harvest management should implement proportional threshold strategies (Lande, Sæther, & Engen, 1997) to avoid unsustainable high harvest rates when populations decline.

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AUTHORS' CONTRIBUTIONS

E.B.N. initiated the work and launched the original research idea. E.B.N., L.F.E. and P.F.M. refined the idea and approach. L.F.E. collected and compiled data from area managers, L.F.E. analysed the data, and L.F.E. and E.B.N. conducted the simulations. L.F.E. wrote the manuscript, and E.B.N. and P.F.M. contributed to the writing. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.n2q50 (Eriksen, Moa, & Nilsen, 2017).

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