ARTICLE

# Retrospective comparisons of competing demographic models give clarity from "messy" management on a Scottish grouse moor

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## Abstract

Retrospective comparison of predictive models that describe competing hypotheses regarding system function can shed light on regulatory mechanisms within the framework of adaptive resource management. We applied this approach to a 28-year study of red grouse (*Lagopus lagopus scotica*) in Scotland, with the aims of reducing uncertainty regarding important drivers of grouse population dynamics, and of evaluating the efficacy of using seasonal versus annual model assessments. We developed three sets of models that predicted pre-breeding and post-breeding grouse density, matching the timing of grouse counts on the ground. We updated conditions and management through time in the spirit of a real-time, adaptive management program and used a Bayesian model weight updating process to compare model predictions with empirical grouse densities. The first two model sets involved single annual updates from either pre-breeding or post-breeding counts; the third set was updated twice a year. Each model set comprised seven models representing increasingly complex hypotheses regarding potentially important drivers of grouse: the baseline model included weather and parasite effects on productivity, shooting losses and density-dependent overwinter survival; subsequent models incorporated the effect of habitat gain/loss (HAB), control of non-protected predators (NPP) and predation by protected hen harriers (*Circus cyaneus*, HH) and buzzards (*Buteo buteo*, BZ). The weight of evidence was consistent across model sets, settling within 10 years on the harrier (NPP + HH), buzzard (NPP + HH + BZ) and buzzard + habitat (NPP + HH + BZ + HAB) models, and downgrading the baseline + habitat, non-protected predator, and non-protected predator + habitat models. By the end of the study only the buzzard and buzzard + habitat models retained substantial weights, emphasizing the dynamical complexity of the system. Habitat inclusion failed to improve model predictions, implying that over the period of this study habitat quantity was unimportant in determining grouse abundance. Comparing annually and

biannually assessed model sets, the main difference was in the baseline model, whose weight increased or remained stable when assessed annually, but collapsed when assessed biannually. Our adaptive modeling approach is suitable for many ecological situations in which a complex interplay of factors makes experimental manipulation difficult.

# INTRODUCTION

Managers who utilize adaptive resource management (ARM; Walters, 1986) develop a formal process that incorporates monitoring in the context of annual decisions and management actions to reduce uncertainties and clarify future decisions. The optimal use of ARM is periodic, in real time (e.g., North American Waterfowl Management Plan; Nichols et al., 2015; Williams et al., 2002) as part of a structured decision process in which predictions from a set of models that describe alternate hypotheses regarding system function are compared with monitoring data. During each cycle, managers are able to update faith in models, as measured by model weights. Models that better predict observed data gain weight, whereas models that perform less well lose weight (Cooch et al., 2014). Over time, managers learn more about system function, which allows them to make better decisions (McGowan et al., 2015; Williams et al., 2002).

Recently, researchers have used a retrospective approach that mimics the process of model comparisons and weight updating in ARM (Dunham & Grand, 2017; McGowan, 2015; Powell et al., 2011; Robinson et al., 2017). Although assessment of monitoring data from previous years does not provide real-time improvements in learning while the data are gathered, retrospective comparison of predictive models that describe competing hypotheses regarding system function can provide unique insights into regulatory mechanisms from a substantial time series of data to provide biological insight as well as guide future management. All of these previous efforts to use retrospective model assessments have used annual monitoring data. Frequency of monitoring has been evaluated from the perspectives of measuring disturbance impact (Liberty et al., 2007), reducing uncertainty in occupancy or species richness estimates (Pease et al., 2021; Sliwinski et al., 2016), and understanding seasonal dynamics (Calvert & Gauthier, 2005; Saunders et al., 2019). The structure of population monitoring in a long-term study of red grouse (*Lagopus lagopus scotica*) in Scotland with two survey periods per year builds on the latter and provides a unique opportunity

to determine whether inclusion of pre- and post-breeding-season counts in a model comparison framework reduces model uncertainty more rapidly than depending on a single count per year.

Red grouse are functionally tied to systems of heather (*Calluna vulgaris*) moors in the uplands of the UK (Jenkins et al., 1963), but many heather-dominated moorlands have undergone conversion to forests or grasslands for sheep grazing during the last century (Thompson et al., 1995). Habitat loss has affected the traditional system of driven red grouse shooting (whereby the birds are pushed by beaters toward a waiting line of guns) that has been the main economic land use on many moors. A "grouse moor" managed for driven shooting is a highly managed system, as gamekeepers are employed to kill generalist predators, including red foxes (*Vulpes vulpes*) and carrion crows (*Corvus corone*), conduct burning to encourage growth of young, more palatable heather, and control parasites of grouse such as sheep ticks (*Ixodes ricinus*) and nematode worms (*Trichostrongylus tenuis*), to maximize the shootable surplus (e.g., Hudson & Newborn, 1995; Lovat, 1911). Raptors were heavily culled historically, and evidence indicates that the illegal killing of raptors persists on many moors managed for grouse despite full legal protection since 1954 (Newton, 2020).

Previous assessments of the studies on red grouse carried out on Langholm Moor in southwest Scotland have emphasized the complexities that complicate disentangling the relative contributions of potential drivers of the system. Research on the system has been non-experimental, and management strategies and associated natural events have been dynamic and unstructured, or "messy" (Dobson et al., 2020) during almost three decades (Figure 1; please refer to Ludwig, Aebischer, Richardson, et al., 2020 for maps of the study site). Grouse bags from shooting, as an index of abundance (Cattadori et al., 2003), have fluctuated historically, but by 1997 numbers had declined to the point that shooting was considered economically unviable and stopped. Active management for grouse at Langholm ended after
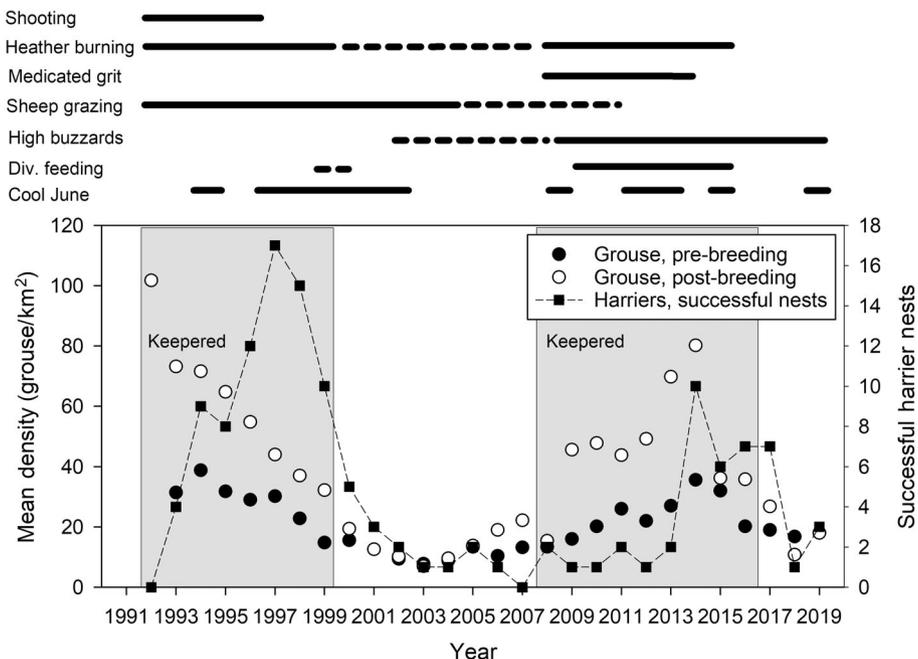
**FIGURE 1** Temporal distribution of management strategies (dashed lines for heather burning and sheep grazing represent reduced levels of those disturbances; keepering occurred during gray-shaded periods and not during unshaded periods), raptor population levels (dashed line for buzzards represents moderate levels), weather events, and mean pre- and post-breeding densities of red grouse at Langholm Moor in southwest Scotland during 1992–2019. Density data from Ludwig, Aebischer, Richardson, et al. (2020).

1999. In 2008, management resumed to attempt to restore red grouse numbers with an eventual goal of shooting, and during this time management has required the investment of >£200,000 per year (Ludwig et al., 2017). An associated long-term study, which started in 1992, resulted in the collection of many types of ancillary data (including habitat, weather, and predator abundance) and production of papers on a variety of aspects of the local red grouse/heather ecosystem (e.g., Ludwig et al., 2017; Redpath & Thirgood, 1997; Thirgood, Redpath, Haydon, et al., 2000). However, despite the investment in management and the information available from the long-term study, managers still have not been able to return grouse numbers to desired levels. Consequently, there is potential to gain insight from application of a post hoc adaptive management framework to address uncertainty about what is driving the system and better understand why management for red grouse was unsuccessful in restoring grouse densities to a level sufficient for driven shooting (Ludwig et al., 2017).

Our goal was two-fold: (1) to reduce uncertainty regarding important drivers of population dynamics of red grouse at Langholm, and (2) to evaluate the efficacy of using seasonal versus annual assessments of models of population dynamics. To this end, we developed sets of models that predicted grouse density at two critical times of year, pre-breeding and post-breeding, and used a Bayesian model weight updating process to compare model predictions with empirical grouse densities from the study site to gain insights into factors influencing red grouse abundance. We predicted that those insights might vary depending on the temporal scale of the models used for evaluation, because the effects of factors active in the first half of the annual cycle could be swamped by the effects of factors active in the second half of the cycle (e.g., Nichols et al., 2015; Powell et al., 2011; Robinson et al., 2017). Given the known importance of keepering to support grouse nest success (Thirgood, Redpath, Haydon, et al., 2000), the rapid transitions in heather on the site (Ludwig, Aebischer, Richardson, et al., 2020), and evidence that some raptors affect survival and productivity of grouse (Ludwig et al., 2017; Redpath & Thirgood, 1997), we expected these three factors to show cumulative effects as drivers of grouse densities.

## METHODS

### Study area

We used 28 years of data from 1992 to 2019 gathered at Langholm Moor (55.219° N, 2.885° W, southwest Scotland), managed for sheep farming and red grouse shooting (Ludwig, Aebischer, Richardson, et al., 2020; Ludwig et al., 2017). Management of red grouse was intended to generate sufficient numbers for driven grouse shooting (Langholm Moor Demonstration Project, 2019; Redpath & Thirgood, 1997). Red grouse were counted in a 42-km$^2$

study site within the 115-km$^2$ Langholm study area, which included most of the 76-km$^2$ Langholm–Newcastleton Hills Special Protection Area designated for breeding hen harriers *Circus cyaneus*. The vegetation on the grouse study site was dominated by heather moorland (dry heath and blanket bog) and surrounded by acidic grasslands (Ludwig, Aebischer, Bubb, Roos, & Baines, 2018). Historically, red grouse bags at Langholm had declined at an average rate of 1.7% per annum during the period 1913–1990 (Thirgood, Redpath, Haydon, et al., 2000), implying a long-term decline in abundance (Cattadori et al., 2003). The conversion of nearly half of the heather moorland to grassland caused by intensive grazing by sheep between 1948 and 1988 seemed likely to have contributed to the decline, as may have other factors such as decreases in numbers of gamekeepers and increases in numbers of predators (Thirgood, Redpath, Haydon, et al., 2000).

From 1992, red grouse densities showed changes associated with a wide array of conditions resulting from dynamic management (Ludwig et al., 2017; Thirgood, Redpath, Haydon, et al., 2000; Figure 1). Starting in 1992, raptors were rigorously protected on the study site, and their numbers generally increased thereafter. Grouse shooting stopped after 1996. The moor was managed by a team of five gamekeepers during 1992–1999 and 2008–2016. The keepers burned and mowed heather for the benefit of grouse and culled predators that could be legally controlled, including mainly red fox, carrion crow, stoat (*Mustela erminea*), and weasel (*Mustela nivalis*). Burning and predator control were very limited during 2000–2007 and ceased after 2016 when there were no keepers. Gamekeepers used medicated grit (Newborn & Foster, 2002) during 2008–2014 to control the intestinal nematode *T. tenuis*, which is known to cause periodic population declines in grouse (Hudson et al., 1998). Initial reductions in sheep numbers from 1990 did not prevent heather decline, but further reductions over a larger area from 2011 led to heather recovery, relative to 1990 levels, by 2015 (Ludwig, Aebischer, Richardson, et al., 2020). Weather and raptor population dynamics added further complexity to this managed system (Figure 1), including two periods in which half (1998–1999) or all (2008–2015) of the hen harrier broods were managed with diversionary feeding to reduce the impact of harriers on grouse productivity (Ludwig, McCluskie, Keane, Barlow, et al., 2018; Redpath et al., 2001). We designed our modeling approach to incorporate information from these patterns (Powell et al., 2022).

## Grouse counts and seasonal models

Red grouse densities (number km$^{-2}$) were estimated as the average of counts in 10 0.5-km$^2$ areas during March/early April (pre-breeding, and spring in the Northern Hemisphere) and July/early August (post-breeding) each year at Langholm, except for spring 1992, spring 2001 and spring 2019. Each count was of grouse flushed by walking along transects 150 m apart with a pointer dog quartering to ~100 m either side of the transect (Thirgood, Redpath, Rothery, & Aebischer, 2000). We used season-specific model sets (Table 1; Appendix S1: Table S1) to describe dynamics of red grouse during the annual cycle: breeding-season models predicted post-breeding density in year $t$ ($D_{pre}^t$) as a function of pre-breeding density ($D_{pre}^t$), annual productivity ($P_t$, juveniles per adult post-breeding), and summer adult survival ($S_s^{ad}$). The non-breeding-season models predicted pre-breeding counts ($D_{pre}^t$) as a function of the previous post-breeding count ($D_{post}^{t-1}$), the bag density from fall shooting ($B_{t-1}$), and summer and winter survival ($S_s^{ad}, S_w$; Appendix S1: Table S1). We structured models as basic "BIDE" (births, immigration, deaths, and emigration) models of population growth, although we ignored immigration and emigration because our study site was isolated from other grouse moors and regarded as effectively closed from a population dynamics perspective (Ludwig, Aebischer, Bubb, Roos, & Baines, 2018; Ludwig, Aebischer, Richardson, et al., 2020). In all years, demographic parameters derived from Langholm Moor were influenced by multiple factors whose effects we sought to evaluate (Figure 1). We started with a baseline model that assumed no effects of presence of keepers. Therefore, to avoid circularity of argument, we parameterized this simplest model with estimates taken from independent studies. To that end, we drew on the Otterburn Experiment (Fletcher et al., 2010, 2013), designed to assess the effect of predator removal by gamekeepers on ground-nesting birds. Grouse demographic data were collected using equivalent methods to Langholm, and we used the "natural" unkeepered situation as a baseline that could be adjusted to Langholm conditions and developed further with additional components corresponding to increasing layers of complexity.

We updated conditions and management during the time series of the project in the spirit of a real-time, adaptive management program (Nichols et al., 2015; Williams et al., 2002). Each set of models included seven models that represented hypotheses with regard to potentially important drivers of grouse density; models were hierarchical in their complexity, in that the most complex models included effects found in simpler models (Table 1). Our model names were typically based on the unique component added to the model (e.g., "buzzard" included baseline effects, non-protected predators, hen harriers, and buzzards). We review model structures in detail below with regard to seasonal components in each model, and we summarize all the model parameter estimates in Table 2.

**TABLE 1** Competing models in three model sets used in the assessment of red grouse population dynamics at Langholm Moor during 1992–2019.

| No. | Model name | Model sets | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **A: Pre-breeding assessments** | | | **B: Post-breeding assessments** | | | **C: Pre- and post-breeding assessments** | | |
| | | Model chain | Start | End | Model chain | Start | End | Model chain | Start | End |
| 1 | Baseline | $D^t_{pre} \to S1 \to W1$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W1 \to S1$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W1, D^t_{pre} \to S1$ | Jul 1992 | Jul 2019 |
| 2 | Baseline + habitat | $D^t_{pre} \to S1 \to W1.5$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W1.5 \to S1$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W1.5, D^t_{pre} \to S1$ | Jul 1992 | Jul 2019 |
| 3 | NPP | $D^t_{pre} \to S2 \to W2$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W2 \to S2$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W2, D^t_{pre} \to S2$ | Jul 1992 | Jul 2019 |
| 4 | NPP + habitat | $D^t_{pre} \to S2 \to W2.5$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W2.5 \to S2$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W2.5, D^t_{pre} \to S2$ | Jul 1992 | Jul 2019 |
| 5 | NPP + HH | $D^t_{pre} \to S3 \to W3$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W3 \to S3$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W3, D^t_{pre} \to S3$ | Jul 1992 | Jul 2019 |
| 6 | NPP + HH + BZ | $D^t_{pre} \to S4 \to W4$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W4 \to S4$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W4, D^t_{pre} \to S4$ | Jul 1992 | Jul 2019 |
| 7 | NPP + HH + BZ + habitat | $D^t_{pre} \to S4 \to W4.5$ | Apr 1993 | Apr 2018 | $D^t_{post} \to W4.5 \to S4$ | Jul 1992 | Jul 2019 | $D^t_{post} \to W4.5, D^t_{pre} \to S4$ | Jul 1992 | Jul 2019 |

*Notes*: Each model set includes seven annual models constructed by linking seasonal components in the appropriate order to predict grouse pre- or post-breeding densities. The first model set (a) takes pre-breeding densities $D^t_{pre}$ as input (shown by the symbol $\to$) into a breeding model (summer, S), the output of which is input to the matching non-breeding model (winter, W), predicting pre-breeding densities 1 year later for assessment of model predictions against actual pre-breeding density estimates; the second model set (b) does the same with post-breeding densities $D^t_{post}$, and the third model set (c) assesses models against both pre- and post-breeding densities. Please refer to *Population Models* section for description of S and W model components. Abbreviations: BZ, buzzard; HH, hen harrier; NPP, non-protected predator.

# Population models

## Baseline model

### *Breeding-season (summer) components*

We set summer (April–July) adult survival in non-keepered years $S^{ad}_{s,nK}$ at 0.6777, the Otterburn Experiment's unkeepered estimate (Fletcher et al., 2013; Table 2). For productivity, research over several decades has consistently recognized the variation caused by weather (Erikstad & Spidsø, 1982; Fletcher et al., 2013; Jenkins et al., 1963; Leslie, 1912), and *T. tenuis* (Dobson & Hudson, 1992; Potts et al., 1984), so we included their effects as follows. We started with the Otterburn Experiment's unkeepered estimate of juvenile/adult ratio of 0.60 (Fletcher et al., 2010), which included the effect of *T. tenuis*. We evaluated the latter using the logistic relationship between productivity $P$ and worms/adult $W$ provided by Potts et al. (1984), relative to productivity with no worms $P_0$:

$$P/P_0 = \left( \frac{e^{(2.217-0.000464W)}}{1 + e^{(2.217-0.000464W)}} \right) / \left( \frac{e^{2.217}}{1 + e^{2.217}} \right) \quad (1)$$

with this equation, the worm effect ranged from 1 without worms to 0.203 (80% reduction in productivity) at 8000 worms/bird (Figure 2b). Using annual worm loads measured in adult shot birds during the Otterburn Experiment (Fletcher, unpublished), we calculated the average

worm effect on productivity to be 0.8846, so corrected Otterburn Experiment's unkeepered estimate of productivity to what it would have been in the absence of worms as $P_{nK} = 0.60/0.8846 = 0.6782$.

Regarding weather, June temperature is especially critical to annual productivity (Hudson, 1992; Slagsvold, 1975), and Slagsvold (1975) reported an average productivity of 2.88 for willow grouse in Norway with a relationship between productivity and annual departure from mean June daily average temperature ($\Delta T_j$) such that $P = 2.88 + 0.53 \, \Delta T_j$. The estimate of unkeepered productivity from the Otterburn Experiment was lower ($P_{nK} = 0.6782$) than Sladsvold's (1975) level of productivity, so we scaled the Slagsvold (1975) equation by $0.6782/2.88$ to ensure that for both old and new equations the same percentage change in temperature led to the same percentage change in productivity. The rescaled equation gave a temperature-dependent estimate of unkeepered productivity in the absence of worms:

$$P^t_{nKT} = 0.6782 + 0.1248 \, \Delta T^t_J$$

where $\Delta T^t_J$ is the annual departure from the mean June daily temperature measured at the Meteorological Office weather station nearest the study site at Eskdalemuir, Scotland, from 1992 to 2019. With $\Delta T^t_J$ ranging from $-1.35$ to $1.60$, $P^t_{nKT}$ ranged from 0.51 to 0.88 (Figure 2a).

To include the effects of *T. tenuis* on productivity (Potts et al., 1984), we multiplied $P^t_{nKT}$ by the worm effect (Equation 1) evaluated at the worm burden $W_t$ in

**TABLE 2** Parameter values and standard errors (SEs) used in stochastic simulation models for red grouse at Langholm Moor during 1992–2019 (please refer to *Population Models* section for detailed descriptions).

| Description | | Value | SE | Source |
|---|---|---|---|---|
| Adult survival April–July, unkeepered | | 0.6777 | 0.0087 | Fletcher et al. (2013), Table 2a |
| Adult survival April–July, keepered | | 0.8782 | 0.0739 | Fletcher et al. (2013), Table 2a |
| Adult survival April–July, BZ effect | | 0.0918 | 0.0198 | Francksen et al. (2019) Table 5 |
| Adult survival April–July, HH effect | c | 0.325 | 0.0214 | Fitted from data in Redpath and Thirgood (1997) |
| Logistic $y = c/(1 + \exp(-b \times [x - m]))$ | b | 0.83 | 0.424 | |
| | m | 6.3 | 0.574 | |
| Young per adult, unkeepered | | 0.60 | 0.09 | Fletcher et al. (2010) p. 268 |
| Young per adult, keepered | | 1.93 | 0.22 | Fletcher et al. (2010) p. 268 |
| Young per adult, Slagsvold | | 2.88 | 0.3166 | Slagsvold (1975), Figure 2 |
| Temperature slope, Slagsvold | | 0.53 | 0.215 | Slagsvold (1975), Figure 3 |
| Worm effect, Otterburn | | 0.8846 | 0.0648 | Fletcher, unpublished data |
| Chick survival, HH effect | c | 0.2986 | 0.0214 | Fitted from data in Redpath and Thirgood (1997) |
| Logistic $y = c/(1 + \exp(-b \times [x - m]))$ | b | 0.83 | 0.424 | |
| | m | 4.755 | 0.574 | |
| Diversionary feeding effect | | 0.811 | 0.053 | From data in Redpath et al. (2001), Ludwig, McCluskie, Keane, Barlow, et al. (2018) |
| Chick survival, BZ effect | | 0.039 | 0.0119 | Francksen et al. (2019) Table 6 |
| Survival October–March, density dependent | a | 0.97 | 0.17 | Thirgood, Redpath, Rothery, and Aebischer (2000) p.512 |
| Relationship $y = a/(1 + bx)$ | b | 0.0172 | 0.0093 | |
| Survival October–March, BZ effect | | 0.088 | 0.021 | Francksen et al. (2019) Table 5 |

*Note*: c, b, m, and a are model coefficients from equations provided in the Description with constant values found or fitted directly from the source literature.
Abbreviations: BZ, buzzard; HH, hen harrier.

year $t$ on Langholm Moor to obtain realized productivity $P_t$:

$$P^t_{nKTW} = P^t_{nKT}\left(\frac{e^{(2.217 - 0.000464W_t)}}{1 + e^{(2.217 - 0.000464W_t)}}\right)/\left(\frac{e^{2.217}}{1 + e^{2.217}}\right) \quad (2)$$

For $W_t$, we used annual mean worm loads from Redpath and Thirgood (1997) and Ludwig, Aebischer, Bubb, Roos, and Baines (2018) for years in which data were available. Generally, worm loads were low, not least because of the use of medicated grit from 2008 onwards (Figure 1), which reduced worm loads in grouse (Newborn & Foster, 2002). In the absence of empirical data during 2000–2007, we used an annual worm load of 200 worms per adult in our models during this time, on the grounds that red grouse densities were lower than during the first keepered period when average annual worm load per adult was 246, reducing the transmission rate, worm load and effects on productivity (Potts et al., 1984). Meaningful reductions in productivity of more than 10% would require a more than eight-fold increase in the worm load (Figure 2b); therefore the potential for bias during model years 2000–2007 is low.

Our baseline model for the breeding season to predict post-breeding densities $D^t_{post}$ of red grouse from pre-breeding densities $D^t_{pre}$ took adult survival $S^{ad}_s = S^{ad}_{s,nK}$ and productivity $P_t = P^t_{nkTW}$ in the general equation:

$$D^t_{post} = D^t_{pre}S^{ad}_s(1 + P_t) \quad (3)$$

*Non-breeding-season components*

Adults and young-of-year red grouse do not differ in post-July survival (Ludwig, Aebischer, Bubb, Richardson, et al., 2018), so for the non-breeding season in all models, we modeled the fate of juveniles and adults combined. Mortality from shooting (Redpath & Thirgood, 1997) and density-dependent winter (October–March) survival (Redpath & Thirgood, 1997) have been established as critical to the long-term dynamics of red grouse. Because bags were low during 1992–1996, shooting would have taken place mostly early in the season, which opens on 12 August; we assumed that shot birds (for which total annual bags were recorded) were removed from the population at the end of August. We also assumed that, excluding shooting losses, monthly survival rate in

August–September was the same as during the 4 months of the breeding season, giving a survival rate for August of $\sqrt[4]{S_s^{ad}}$ and a survival rate for August–September of $\sqrt{S_s^{ad}}$. Therefore the predicted number of red grouse at the start of October, taking the bag $B_{t-1}$ into account, was:
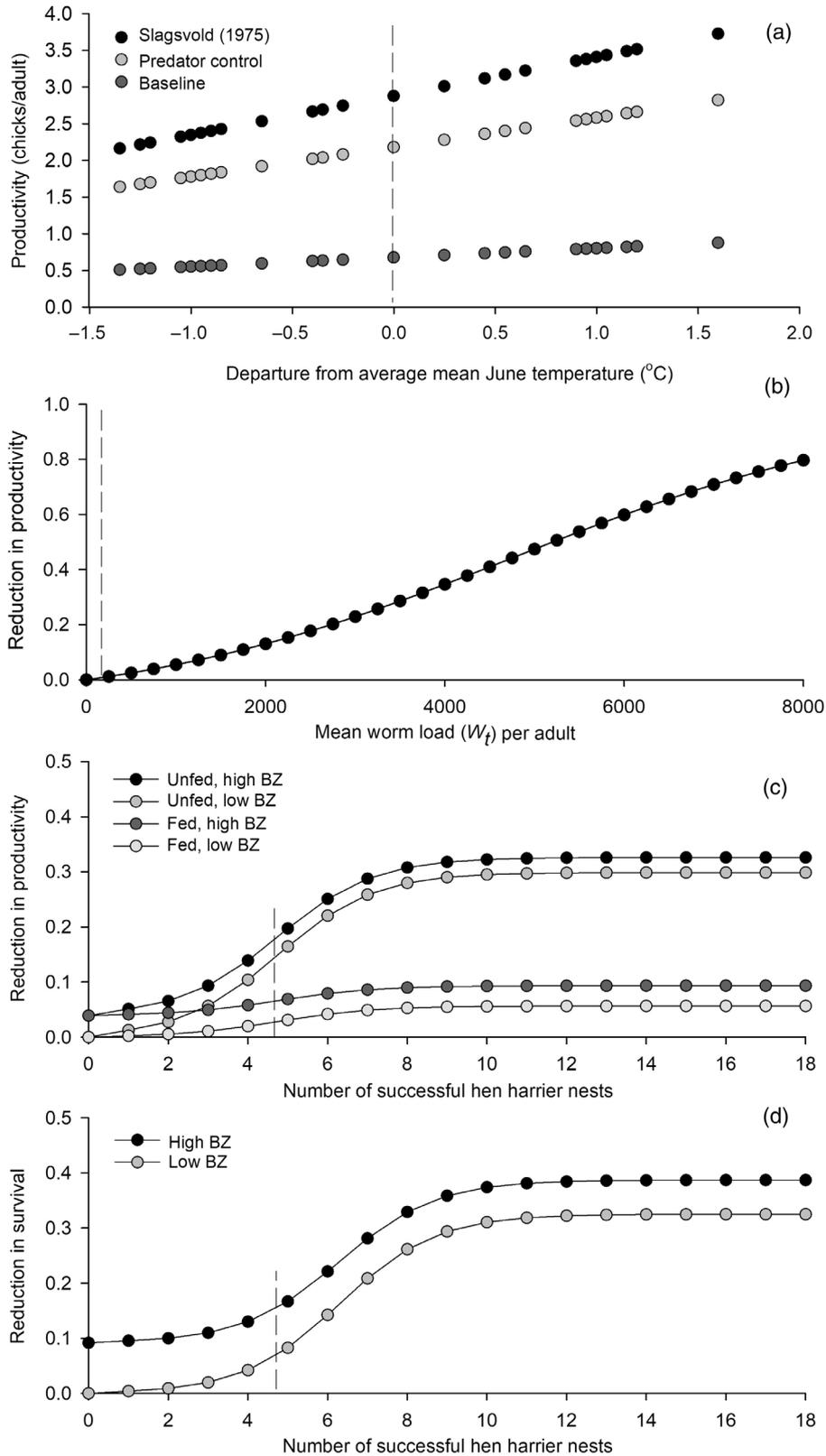


**FIGURE 2** Legend on next page.

$$D_{oct}^t = D_{post}^t \sqrt{S_s^{ad}} - B_t \sqrt[4]{S_s^{ad}} \qquad (4)$$

We used a density-dependent relationship (Thirgood, Redpath, Rothery, & Aebischer, 2000) to predict pre-breeding densities of red grouse at Langholm during 1992–2019 from October densities. As the relationship was expressed in terms of numbers per 0.5 km², we turned it into a survival rate by dividing by (October density)/2:

$$S_{w,dd} = \frac{\left( \frac{0.97 \left( D_{oct}^{t-1}/2 \right)}{1 + 0.0172 \left( D_{oct}^{t-1}/2 \right)} \right)}{D_{oct}^{t-1}/2} = \frac{0.97}{1 + 0.0172 \left( D_{oct}^{t-1}/2 \right)} \qquad (5)$$

For reference, deterministic predictions for 6-month winter survival ranged from 0.55 to 0.93 at post-shooting densities of 5–90 grouse/km² (Figure 3b), and Thirgood, Redpath, Rothery, and Aebischer (2000) reported that mean winter survival during 1992–1998 at the study site was 0.67.

The baseline model was obtained by setting $S_s^{ad} = S_{s,nK}^{ad}$ and $S_w = S_{w,dd}$ in the generic model for non-breeding-season dynamics predicting pre-breeding counts of red grouse:

$$D_{pre}^t = D_{oct}^{t-1} S_w \qquad (6)$$

## Habitat model (baseline + habitat)

Red grouse are habitat specialists (Jenkins et al., 1963), and heather cover can predict variation in local abundance of grouse at a regional level (Thirgood et al., 2002). At Langholm, heather loss since the 1940s was the most probable cause of declines in grouse bags over the ensuing 50 years (Redpath & Thirgood, 1997; Thirgood, Redpath, Haydon, et al., 2000), and a primary concern for present management and conservation efforts (Ludwig, Aebischer,

Richardson, et al., 2020). Although habitat did not affect winter survival per se, red grouse natal dispersal was toward areas with greater heather cover, resulting in greater apparent winter losses in areas with lower heather cover (Ludwig, Aebischer, Bubb, Richardson, et al., 2018; Thirgood et al., 2002). Summer survival and productivity of red grouse were unrelated to heather cover (Campbell et al., 2002; Ludwig, Aebischer, Bubb, Richardson, et al., 2018; Redpath & Thirgood, 1997). We therefore extended the baseline model by including habitat effects only in the non-breeding-season component and followed methods of Redpath and Thirgood (1997) to model adult winter survival as a function of carrying capacity. We developed an index of carrying capacity using the proportion of quadrats with heather present from vegetation surveys conducted on the areas used to count grouse in 1997, 2007, 2012, 2015 and 2018 (Ludwig, Aebischer, Richardson, et al., 2020), combined with an estimate of change between 1988 and 1994 from Redpath and Thirgood (1997). We used interpolated heather extent across years among vegetation surveys using an exponential model to estimate the slope coefficient:1992–1994 coefficient: −0.021; 1997–2007: −0.030; 2007–2012: 0.015; 2012–2015: 0.089; 2015–2018: −0.025. We extended the model for the periods 1995–1996 and 2019 by extending the trend for 1992–1994 and 2015–2018 respectively (Figure 3a). We calculated carrying capacity as the proportion, $H$, of heather extent relative to the estimated extent in 1992, the first year of our study, and in the predictive model (Equation 6) set $S_w = H S_{w,dd}$.

## Non-protected predator (NPP) model

### Breeding-season components
We modified the baseline model to describe the additional effects of non-protected predators on productivity and survival. Gamekeepers have been shown to reduce fox and crow abundance by 43% and 78% respectively

**FIGURE 2** Breeding-season model components used to predict red grouse densities at Langholm Moor in southwest Scotland, shown as deterministic relationships. (a) For productivity as influenced by departure from average mean June temperature (set to 0, marked by dotted line) for temperatures observed during the study: as predicted for willow grouse in Norway (Slagsvold, 1975; solid circles); as standardized relative to worm-free red grouse productivity in the baseline and non-protected predator situations (Fletcher et al., 2010, open and gray circles respectively). (b) For proportional reduction in red grouse productivity due to average load per adult of the parasitic worm *Trichostrongylus tenuis* (from Potts et al. (1984); dotted line represents average worm load observed during our study). (c) For proportional reduction in red grouse productivity in relation to number of successful hen harrier nests (from Redpath & Thirgood, 1997), according to the use of diversionary feeding (open circles: nests fed, solid circles: nests unfed) and buzzard abundance (solid line: low buzzard abundance, dashed line: high buzzard abundance); vertical line indicates average number of hen harrier nests during the study period. (d) For proportional reduction in adult survival (solid circles) of red grouse in relation to the number of successful hen harrier nests (from Redpath & Thirgood, 1997), according to buzzard (BZ) abundance (solid line: low abundance, dashed line: high abundance); vertical line indicates the average number of hen harrier nests during the study period.
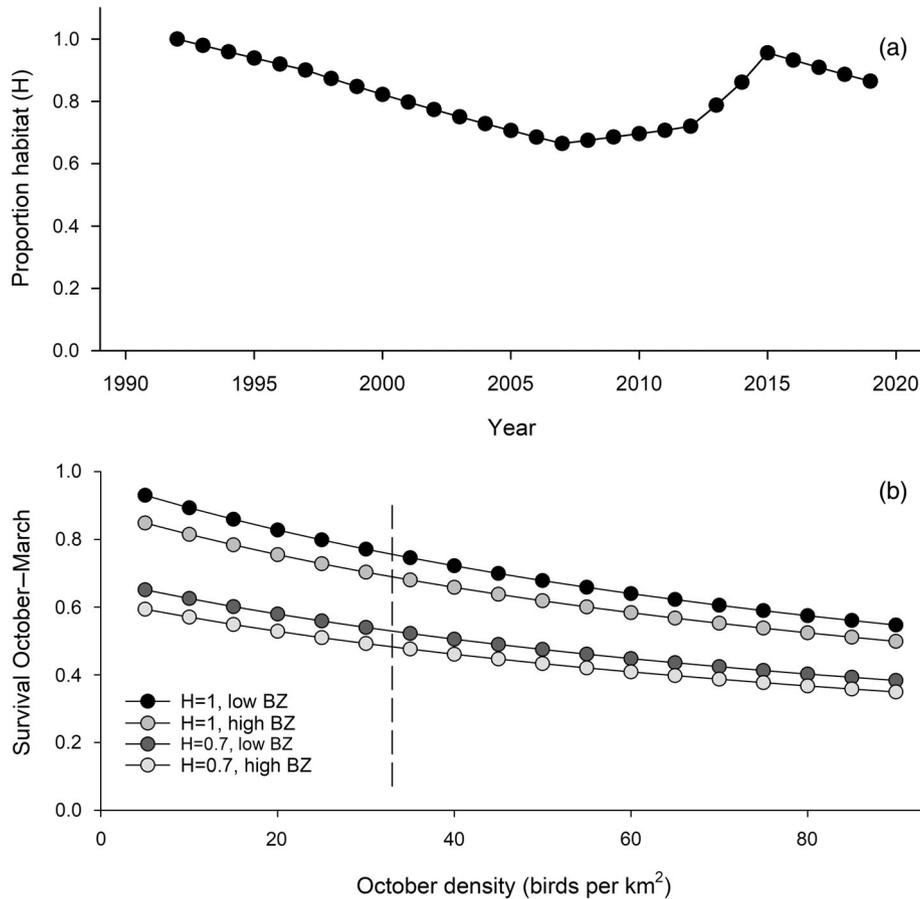
**FIGURE 3** Non-breeding-model components used to predict red grouse densities at Langholm Moor in southwest Scotland during 1992–2019. (a) Proportional carrying capacity (*H*) as a result of reduction and eventual restoration of area covered by heather (Ludwig, Aebischer, Richardson, et al., 2020). (b) Density-dependent survival of red grouse from October to March (from Thirgood, Redpath, Rothery, & Aebischer, 2000) for the range of October densities observed during the study, in relation to two levels of proportional carrying capacity (solid circles: *H* = 1, open circles: *H* = 0.7) and buzzard (BZ) abundance (solid line: low abundance, dashed line: high abundance). Vertical line indicates average October grouse density during the study period.

(Fletcher et al., 2010). Langholm had four distinct periods in which the moor was keepered (1992–1999), not keepered (2000–2007), again keepered (2008–2016), and again unkeepered (2017–2019). Although the long-term studies at Langholm have collected annual indices or counts of foxes, crows, and weasels, there is no direct, per capita measure of their proportional effect on grouse productivity. Therefore, we used the presence or absence of gamekeepers as a discrete function to predict levels of productivity.

During years of game keeping at Langholm, we used an estimate of 4-month summer survival $S_{s,K}^{ad}$ of 0.8782 resulting from the Otterburn Experiment when keepered (Fletcher et al., 2013; Table 2). For productivity during keepered years, the Otterburn Experiment estimated the juvenile/adult ratio at 1.93, which was 3.2167 times higher than its unkeepered estimate of 0.60 (Fletcher et al., 2010). We incorporated this amplification in

magnitude into the structure of our model, using a discrete variable, $I_K$ (not keepered: $I_K = 0$; keepered: $I_K = 1$), to switch between keepered and unkeepered situations. We defined $S_s^{ad}$ and $P_t$ in Equation (3) as:

$$S_s^{ad} = S_{s,nK}^{ad}(1 - I_K) + S_{s,K}^{ad} I_K \quad (7)$$

$$P_t = P_{nKTW}^t((1 - I_K) + 3.2167 I_K)$$

*Non-breeding-season components*

Fletcher et al. (2013), who experimentally assessed the effect of removing non-protected predators while holding other factors constant, found that with predator removal, change in grouse numbers between consecutive springs was not explained by change in numbers over the non-breeding period, but only by breeding-season parameters. The version of Equation 4 used in the non-breeding-

season component of the NPP model therefore uses the $S_s^{ad}$ value of Equation 7, and the version of Equation 6 uses $S_w = S_{w,dd}$ as in the baseline model.

## Non-protected predator + habitat model (NPP + habitat)

The habitat effect, as described for the baseline + habitat model, was added to the NPP model. Therefore, for this model the structure of the predictive model (Equations 3, 4, 6) used $S_s^{ad}$ as defined in Equation (7) and a habitat-specific modification of $S_w = HS_{w,dd}$.

## Harrier model (NPP + HH)

### Breeding-season components

Raptors are protected by law, and research from Langholm has shown the effects of hen harriers and peregrine falcons (*Falco peregrinus*) on adult survival and productivity of red grouse (Thirgood, Redpath, Rothery, & Aebischer, 2000). More recent work has also implicated buzzards (*Buteo buteo*) (Francksen et al., 2019). Buzzard numbers were low at Langholm initially and hen harrier and peregrine were the primary avian grouse predators during 1992–1996 (Thirgood, Redpath, Rothery, & Aebischer, 2000). Unlike hen harrier numbers, peregrine numbers at Langholm were fairly stable, and their average density of 2.3 nests per $100\,km^2$ (Ludwig, Roos, Rollie, & Baines, 2020) was similar to that during the Otterburn Experiment (Fletcher, unpublished). We therefore considered that the effect of peregrine predation was already included in the baseline model, and here modified the NPP model to describe the additional effects of hen harriers on breeding-season dynamics of red grouse.

We used numbers of female hen harriers that successfully bred at Langholm (Ludwig, Roos, Rollie, & Baines, 2020) when modeling grouse productivity, because hen harriers commonly feed grouse chicks to their young, unlike peregrines. Redpath and Thirgood (1997) calculated grouse productivity at Langholm with and without harriers in 1995 and 1996; we applied their approach to their 1993–1994 data and derived a logistic relationship linking the proportional decrease in grouse productivity $L^P_{HH}$ occasioned by harriers to the number HH of successful harrier nests:

$$L^P_{HH} = \frac{0.2986}{1 + e^{0.830(HH-4.755)}}$$

Predicted decrease in grouse productivity, $L_{HH}$, ranged from 0 when there were no hen harriers to 0.30 when the number of successfully breeding hen harriers exceeded 15 (Figure 2c). We incorporated the effects of diversionary feeding, noting that its effect was to reduce the offtake of grouse chicks by harriers by 81.1% (average of 1998–1999 values from Redpath et al., 2001 combined with camera and pellet values for 2008–2015 from Ludwig, McCluskie, Keane, Barlow, et al., 2018, estimated following Redpath & Thirgood, 1999), by assuming that the harrier-induced decrease in grouse productivity $L_{HH,DF}$ diminished according to the proportion DF ($0 \le DF \le 1$) of successful female harriers that were fed (Figure 2c):

$$L^P_{HH,DF} = (1 - 0.811\,DF)\,L^P_{HH}$$

We calculated harrier-affected productivity by modifying productivity in the baseline model (Equation 3) as:

$$P_t = P^t_{nKTW}\left((1-I_K) + 3.2167\,I_K\right)\left(1 - L^P_{HH,DF}\right)$$

Hen harriers can also affect the survival of adult grouse during the breeding season. To model this, we adjusted the logistic relationship obtained for productivity by calibrating it against estimates of the proportional decrease in adult survival due to harriers obtained from Redpath and Thirgood's (1997) evaluation of adult survivorship in 1995 and 1996 with and without harriers (Figure 2d):

$$L^S_{HH} = \frac{0.325}{1 + e^{0.83(HH-6.30)}}$$

We calculated harrier-affected adult survival for use in the predictive model (Equation 3) as

$$S_s^{ad} = \left[S_{s,NK}^{ad}(1-I_K) + S_{s,K}^{ad}I_K\right]\left(1 - L^S_{HH}\right) \qquad (8)$$

### Non-breeding-season components

The density-dependent relationship for $S_{w,dd}$ incorporated the effects of peregrines and hen harriers present over winter at Langholm. Breeding peregrine numbers at Langholm remained low throughout the study (Ludwig, Roos, Rollie, & Baines, 2020), wintering hen harrier numbers were unrelated to breeding numbers, and many wintered elsewhere (Ludwig, Roos, Rollie, & Baines, 2020; Redpath & Thirgood, 1997). Therefore, for the predictive model (Equation 6) we assumed that $S_w = S_{w,dd}$ remains the same in the presence of hen harriers, while $S_s^{ad}$ in Equation (4) took the same value as in the equivalent harrier summer model (Equation 8).

## Buzzard model (NPP + HH + BZ)

### Breeding-season components

The potential for effects of buzzards on red grouse is more uncertain than the effect of hen harriers, and buzzard numbers were fairly low at Langholm during 1992 to 1996 (Ludwig, Roos, Rollie, & Baines, 2020). However, they increased during 1992–2018 (Ludwig, Roos, Rollie, & Baines, 2020), and Francksen et al. (2019) calculated the extent to which buzzards may have had an effect on red grouse numbers. In an adaptive fashion, we added effects of buzzards to the NPP + HH model to account for buzzards' potential limiting dynamics. As such, this model then accounted for the full slate of predator effects.

Numbers of buzzard nests were not monitored consistently, so we used buzzard survey data based on sightings during breeding-bird transect surveys (Ludwig, Roos, Rollie, & Baines, 2020). Because the index of buzzard abundance thus obtained varied highly from year to year, we described the local buzzard population as low in years with a 5-year moving average of sightings/km below 0.10 (1992–1999), moderate at 0.10–0.15 (2000–2007), and high above 0.15 (2008–2019; Figure 1). We modeled productivity with a 3.9% decrease during high buzzard (BZ = 1) years (average of Francksen et al. (2019)'s estimates of the percentage of grouse chicks consumed by buzzards at Langholm). During years with moderate levels of buzzards (BZ = 0.5; Figure 1), we decreased productivity by one-half of the effect during high buzzard years. Years in which buzzard numbers were classified as low (BZ = 0) represented the baseline, and we did not decrease productivity (noting that buzzards had also been present at low density in the Otterburn Experiment, so low-level buzzard effects were included in the baseline parameters). We modeled adult grouse survival with a 9.2% decrease during high buzzard years (average of Francksen et al. (2019)'s estimates of the percentage of adult grouse consumed by buzzards at Langholm), reduced by half then to zero in moderate and low years respectively. In both cases our approach assumed that buzzards killed the grouse that they ate; an alternative hypothesis, that buzzards scavenged grouse that died for other reasons, is equivalent to the NPP + HH model).

Our survival and productivity parameters for the combined non-protected predator, hen harrier and buzzard models for the predictive model for the breeding season (Equation 3) were:

$$S_s^{\mathrm{ad}} = \left[ S_{s,nK}^{\mathrm{ad}}(1 - I_K) + S_{s,K}^{\mathrm{ad}} I_K \right] \left(1 - L_{\mathrm{HH}}^S\right)(1 - 0.092\,\mathrm{BZ}) \quad (9)$$

$$P_t = P_{nKTW}^t\left((1 - I_K) + 3.2167\,I_K\right)\left(1 - L_{\mathrm{HH,DF}}^P\right)(1 - 0.039\,\mathrm{BZ})$$

### Non-breeding-season components

We used the same approach to quantifying buzzard population levels during the study as in the breeding-season harrier/buzzard model. In years in which buzzard numbers were high, we decreased adult survival over winter by 8.8% following estimates of winter mortality from buzzards by Francksen et al. (2019), giving $S_s^{\mathrm{ad}}$ (Equation 4) the same value as in the equivalent buzzard summer model (Equation 9) and modifying $S_w$ in Equation (6) as follows:

$$S_w = S_{w,\mathrm{dd}}(1 - 0.088\,\mathrm{BZ})$$

## Buzzard + habitat model (NPP + HH + BZ + habitat)

The habitat effect was added to the NPP + HH + BZ model that included the effects of all grouse-eating raptors. For the predictive model (Equations 3, 4, and 6), we defined $S_s^{\mathrm{ad}}$ as in Equation (9) and we set $S_w = HS_{w,\mathrm{dd}}(1 - 0.088\mathrm{BZ})$.

## Model sets and annual models

The availability of grouse count data from two times during the annual cycle allowed us to test hypotheses related to the speed of learning from twice-annual model comparisons compared with single, annual counts and comparisons (e.g., Nichols et al., 2015; Powell et al., 2011; Robinson et al., 2017). In addition, we saw the potential to assess how seasonal factors might emerge or be swamped, depending on which seasonal count was used in our scenarios using single, annual counts. Our expectation was that twice-annual model comparisons would provide opportunity for model uncertainty to be reduced quicker than once-annual comparisons. In addition, because of overwinter density dependence, we hypothesized that assessments using pre-breeding densities alone were likely to underplay the factors that primarily affected summer survival and breeding success (as they occurred before overwinter density dependence), and to emphasize those that acted over winter to modify the density-dependent relationship (e.g., Boyce et al., 1999; Figure 1). Conversely, post-breeding assessments alone should see the effect of habitat, potentially important in the winter, over-ridden or masked by factors linked to adult summer survival and productivity (e.g., Stenseth et al., 2003), such as the control of non-protected predators and raptor abundance. Independent, twice-yearly assessments should be the most sensitive, offering winter

and summer factors an equal opportunity to influence the model weightings.

We therefore created three sets of the seven annual models described above (Table 1). The first two sets reproduced the standard approach in adaptive management modeling of updating models once a year from actual counts: the first set was anchored on pre-breeding densities, starting with the first pre-breeding estimate in 1993, so used predicted values from breeding-season models (Equation 3) as input into the matching non-breeding-season models (Equation 4 feeding into Equation 6) to predict pre-breeding densities a year later for comparison with actual pre-breeding density estimates; the second set was anchored on post-breeding densities, starting with the first post-breeding estimate in 1992, and used predicted values from non-breeding-season models (Equations 4, 6) as input into the matching breeding-season models (Equation 3) to predict post-breeding densities a year later for comparison with actual post-breeding density estimates. The third set made full use of available data and updated its model weights twice a year from pre- and post-breeding densities, starting with the 1992 post-breeding density, and using actual density estimates as input into first non-breeding (Equations 4, 6) and then matching breeding-season models (Equation 3), with a comparison of predicted densities against actual density estimates at each stage.

## Simulations and model weighting

We used 500 simulations with baseline survival and productivity components of the model structure (Table 2) selected from distributions to introduce demographic stochasticity into the model predictions. During each simulation, we modified the stochastic survival and productivity with the effects inherent in each model's structure.

We then compared the predicted annual or seasonal density for year $t$ and a given simulation with the corresponding actual empirical density to assess the model's predictive value (Figure 4; Appendix S1: Figures S1–S7). Deviations of predicted values from observed values (Figure 5) affected the faith in, or evidence in support of, a given model, and all models began with equal model weight (1.0/7 = 0.14; Figure 6).

In an ARM framework, the model with a predicted density that was closest to the empirical density obtained from monitoring is deemed to have performed best in that iteration (Williams et al., 2002). Therefore, we calculated the mean difference across 500 simulations ($\Delta D_i$) between the $i$th predicted density from the simulation and the appropriate empirical density ($D_{pre}^t, D_{post}^t$) to

modify the model weight during each iteration (Figure 5). We established a probability density function (Powell et al., 2011; Williams et al., 2002) with a normal distribution ($\mu = 0$) using the standard deviation of each season's empirical density. At each iteration $j$ we used the deviation from each simulation, $\Delta D_i$, to calculate the conditional probability, $P_x^{i,j}$, for model $x$, and simulation $i$. We then calculated the mean conditional probability, $\overline{P}_x^j$, across the 500 simulations for each iteration and model. Values of mean conditional probabilities were highest when predictions were closest to the observed count (minimum $\Delta D_i$) and lowest when model predictions deviated from the observed count (maximum $\Delta D_i$).

Next, we used the mean conditional probabilities for the competing models in a given iteration to update our faith in the models within each model set (Table 1). Using Bayes Theorem, the new weight, $w_x^j$, of each model $x$ of the seven models in the model set at iteration $j$, is:

$$w_x^j = \frac{w_x^{j-1} \times \overline{P}_x^j}{\sum\limits_{x=1}^{7} w_x^{j-1} \times \overline{P}_x^j}$$

This function uses the previous iteration's weight for a model ($w_x^{j-1}$), modified by the new conditional probability at iteration $j$ ($\overline{P}_x^j$), relative to the weighted probability of all seven models and their conditional probability (Williams et al., 2002). Cumulative model weights for each model in each model set through time were then calculated in turn (Figure 6). Updates and projections requiring the missing 2001 spring count were not available, so model weights were carried forward unchanged to the next iteration, at which updating was again possible. Model weights at any given period sum to 1.0 across the seven models, and the models' weights represent relative faith in each model's predictions (Nichols et al., 2007).

## RESULTS

### Models assessed once a year, pre-breeding

Because of missing pre-breeding densities in 1992, 2001 and 2019, assessments started in 1994, and were not possible for 2001, 2002 and 2019. Predictions from both the baseline and baseline + habitat models underestimated pre-breeding densities, whereas those from the non-protected predator (NPP) and non-protected predator + habitat models overestimated them, especially during keepered periods (Figures 4a and 5 left). Predictions from the harrier (NPP + HH), buzzard (NPP + HH + buzzard) and buzzard + habitat (NPP + HH + buzzard + habitat)
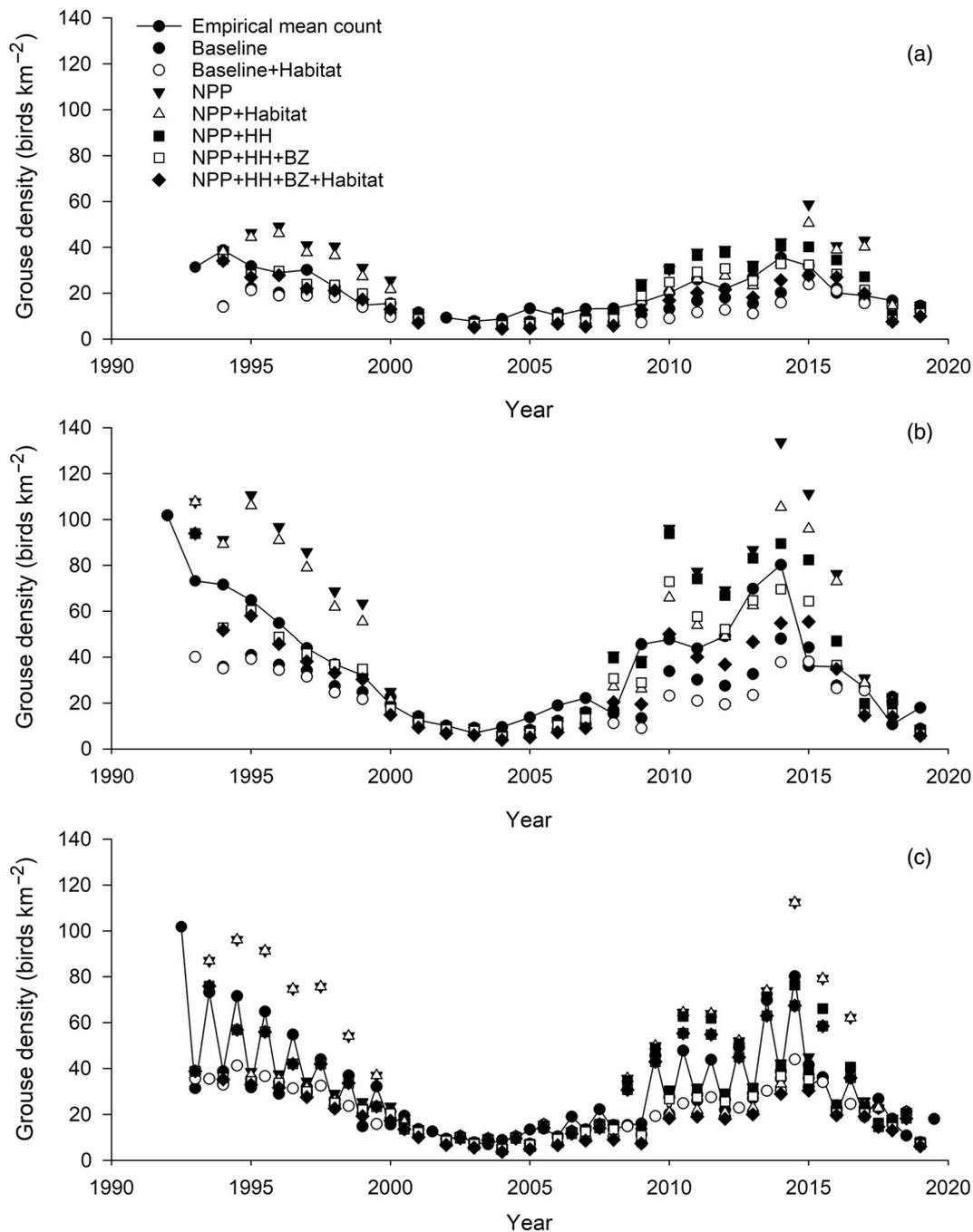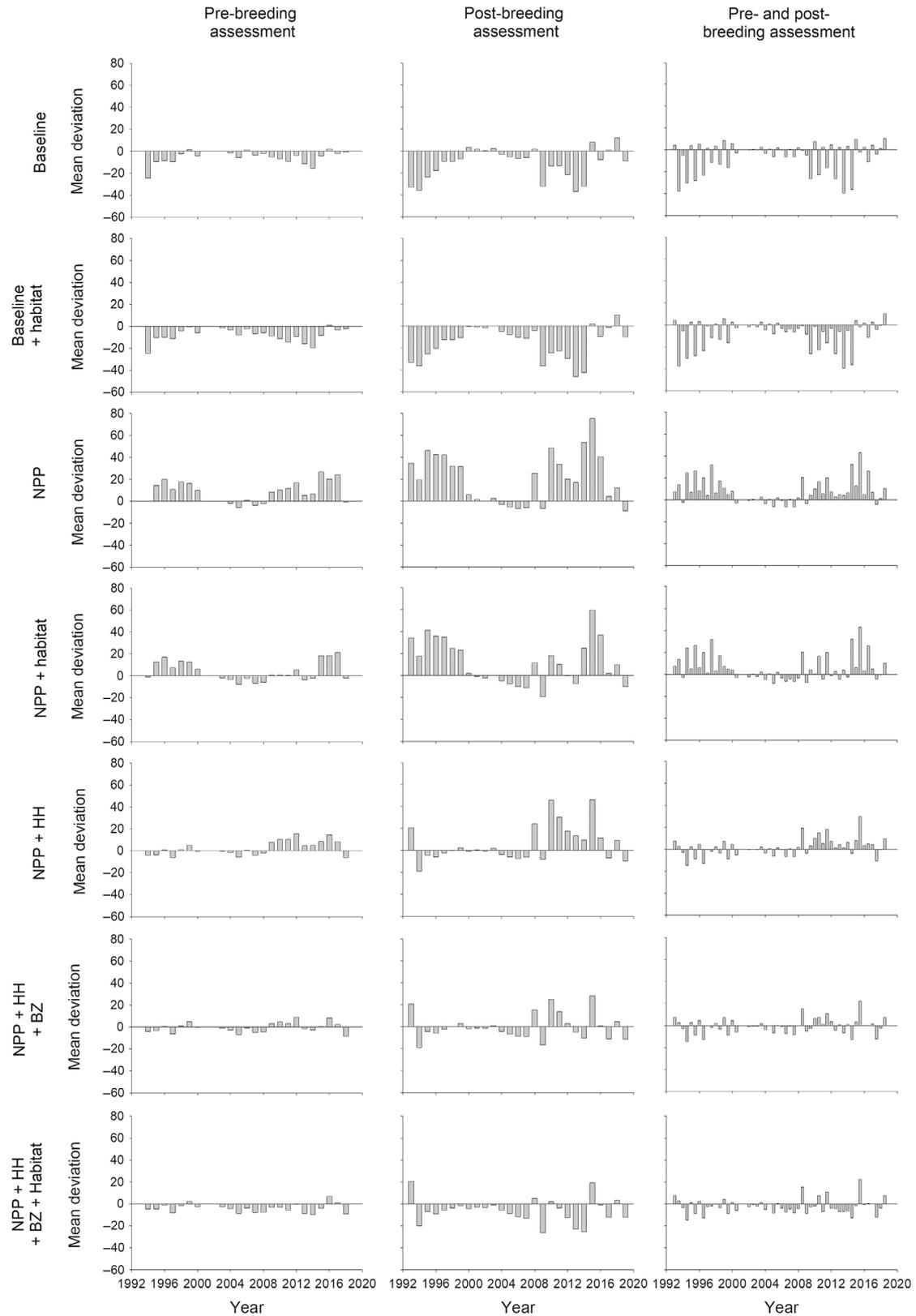
**FIGURE 4** Observed and predicted densities of red grouse at Langholm Moor in southwest Scotland during 1992–2019 from seven competing models in three model sets: (a) models assessed annually pre-breeding; (b) models assessed annually post-breeding; (c) models assessed seasonally both pre- and post-breeding. Model predictions are means from 500 stochastic simulations and are shown with the observed mean density for each year. No pre-breeding density estimates were available for 1992, 2001, or 2019.

models were much better, although the harrier (NPP + HH) model produced overestimates during the second keepered period, and the buzzard + habitat (NPP + HH + buzzard + habitat) model predictions were close to the counts, but biased low (18 out of 21 deviations negative; Figures 4a and 5 left).

The relative evidence from weights (Figure 6a) indicated that models that included the effect of habitat and

the effect of predator control alone (baseline + habitat, non-protected predator, and non-protected predator + habitat models) were poorly supported (weights <0.1). Up to 2003, support for the harrier (NPP + HH), buzzard (NPP + HH + buzzard) and buzzard + habitat (NPP + HH + buzzard + habitat) models was similar. By 2010 the buzzard + habitat model weights were half those of the other two models; but thereafter support for the

**FIGURE 5** Mean deviations of model predictions from observed densities of red grouse at Langholm Moor in southwest Scotland during 1992–2019 for seven competing models in three model sets: models assessed annually pre-breeding (following winter), models assessed annually post-breeding (following summer), models assessed seasonally both pre- and post-breeding. Deviations are means from 500 stochastic simulations. Model components were added to baseline model structure in increasing order of complexity; please refer to *Population Models* section for model structure and descriptions.
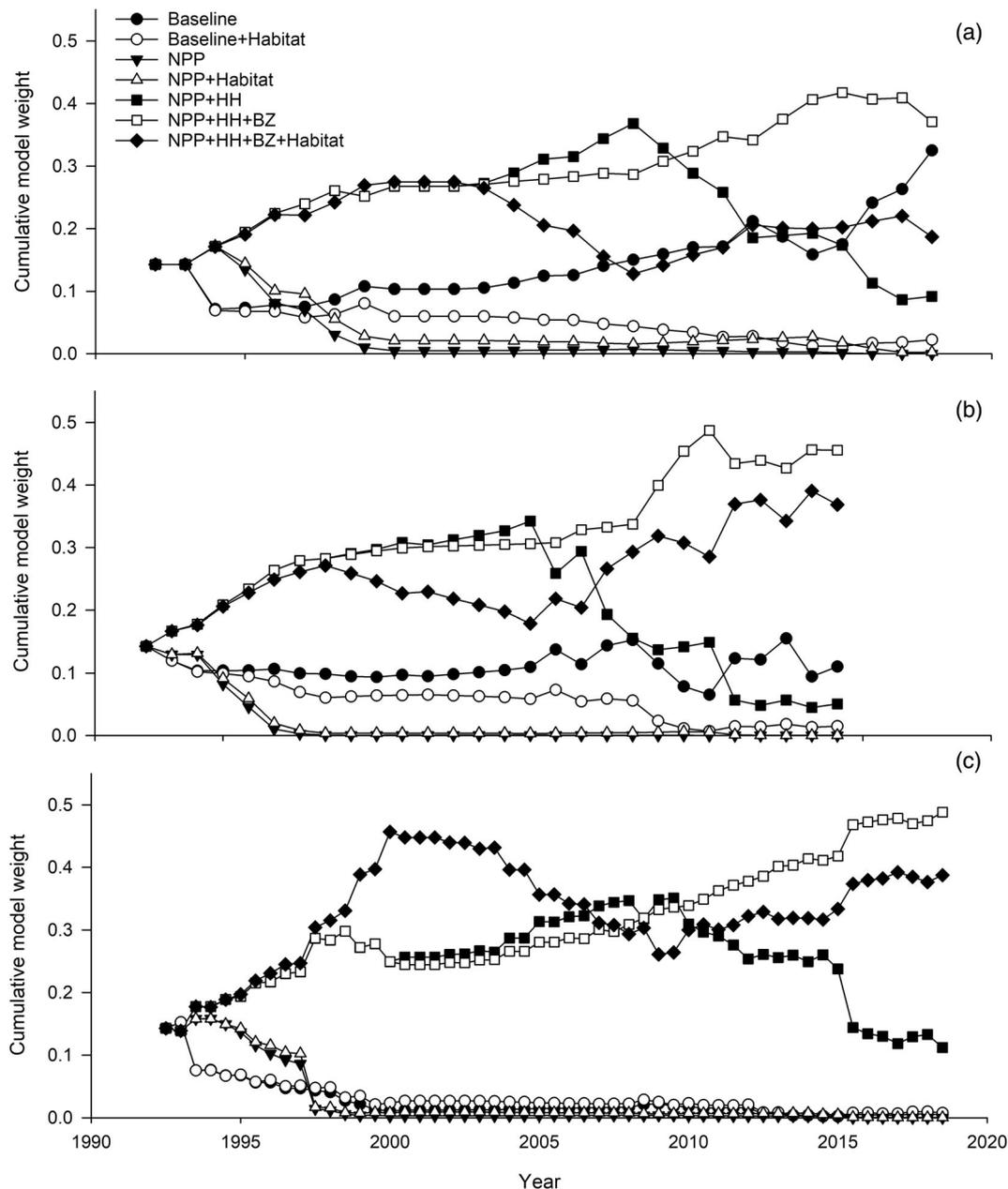
**FIGURE 6** Cumulative model weights of seven competing models used to predict the densities of red grouse at Langholm Moor in southwest Scotland during 1992–2019, in three model sets: (a) models assessed annually pre-breeding, (b) models assessed annually post-breeding, (c) models assessed seasonally both pre- and post-breeding. More positive model weights indicate more relative evidence for the dynamics represented by the structure of a given model. Model components were added to baseline model structure in increasing order of complexity; please refer to text for model structure and descriptions.

harrier model collapsed, leaving the buzzard model as the consistently best model, reaching weights above 0.4 (Figure 6a). In the last 3 years of the series, when keepering had stopped, predictions from the baseline model were closest to the observed counts (Figure 5 left), leading to a rapid increase in weights (Figure 6a) even though the baseline model's performance had previously been poor.

## Models assessed once a year, post-breeding

Annual post-breeding densities were available for the full period 1992–2019, so assessments started in 1993 and were repeated for every year thereafter.

Mirroring the case of annual pre-breeding assessments, the baseline and baseline + habitat models both underestimated post-breeding densities, and the non-protected

predator and non-protected predator + habitat models both overestimated them during keepered periods (Figures 4b and 5 middle). Again, the harrier, buzzard and buzzard + habitat models performed much better, although the harrier model overestimated counts during the second keepered period, and the buzzard + habitat model was biased low, with 22 out of 27 negative deviations (Figure 5 middle).

In terms of model weights (Figure 6b), the relative evidence from weights for the non-protected predator and non-protected predator + habitat models quickly dropped to near zero. Weights for the baseline + habitat model were all below 0.1 and declined to near zero as well, while those for the baseline model remained close to 0.1 throughout the study period. The buzzard model produced the most consistently high weights, ending the period above 0.4. Weights for the buzzard + habitat model dropped after 1998, but increased when keepering resumed, remaining below but roughly parallel with the weights from the buzzard model. The harrier model weights remained very close to those from the buzzard model until keepering resumed in 2007, then support collapsed.

## Models assessed twice a year, pre- and post-breeding

With twice-annual assessments, the first pre-breeding assessment was in 1993 and the last post-breeding one in 2018; no pre- or post-breeding assessment was possible in 2001. Across all models and years, the amount of variation in predictions from models assessed twice a year was on average approximately two-thirds of that in predictions from models assessed once a year (Appendix S1: Figures S1–S7).

The predictions from summer baseline and baseline + habitat models were considerably lower than post-breeding densities during keepered periods, whereas the non-protected predator and non-protected predator + habitat models consistently overestimated post-breeding densities (Figures 4c and 5 right). The remaining three models were more balanced, although the harrier model seemed to overestimate both pre- and post-breeding densities during the second keepered period, and the buzzard + habitat model tended to slight underestimation with 35 out of 48 deviations negative (Figures 4c and 5 right).

The cumulative weights produced a clear dichotomy among the first four models, for which the relative evidence was close to zero from 1999 onwards (Figure 6c). The last three models all gained in weight until 1997, when the buzzard + habitat model climbed to a weight of 0.46 by 2000 (mainly driven by good pre-breeding predictions in 1999 and 2000), only to decline thereafter and drop below the harrier and buzzard models by the start of the second keepered period. From 2009 onwards, support for the harrier model fell away (ending with a weight close to 0.1), whereas support for the buzzard model continued to grow toward a weight of 0.5. The buzzard + habitat model also recovered, to a weight close to 0.4.

## DISCUSSION

### Assessing models once versus twice a year

The inferences from our modeling exercise did not differ substantially among our three sets of annual models (the first updated post-breeding, the second updated pre-breeding, the third updated both pre- and post-breeding) Although we had predicted that early dynamics in the annual cycle could be swamped by effects of factors active in the fall and winter, we did not see a greater prominence of the winter habitat factor in the pre-breeding model set (Figure 6a). Furthermore, we did not see a greater prominence of the summer effects of non-protected predator control or harrier abundance in the post-breeding model set (Figure 6b). Instead, the weight of evidence in all three model sets was markedly consistent (Figure 6a–c), rapidly settling on three models within the first half of the study, namely the harrier (NPP + HH), buzzard (NPP + HH + buzzard) and buzzard + habitat (NPP + HH + buzzard + habitat) models, and rapidly downgrading three models, i.e., the baseline + habitat, non-protected predator, and non-protected predator + habitat models; the latter were downgraded faster under the biannually assessed model set than under the annually assessed ones, probably because there was less variation in model predictions when using biannual assessments. In the second half of the study the evidence for the downgraded models continued to decline and the evidence for the harrier model collapsed, leaving only the buzzard and buzzard + habitat models with substantial weights. The main difference between the annually assessed model sets and the biannually assessed one was in the baseline model, which progressively gained weight when assessed only pre-breeding (Figure 6a), maintained a roughly static weight when assessed only post-breeding (Figure 6b), but was quickly downweighted to near zero when assessed twice a year (Figure 6c).

Some insight into the reasons underlying the changes in model weights over time came from the differences between the model predictions and the counts (Figure 5). For all three model sets, the pattern of deviations was clearly non-random relative to zero for the four downgraded models, with the baseline and baseline + habitat

models too pessimistic in their predictions, and for the non-protected predator and non-protected predator + habitat models over-compensating, so that they were too optimistic during keepered periods. The significant departures of baseline model predictions from actual densities (Figure 5) implied greater complexity in red grouse population dynamics at Langholm than during the Otterburn Experiment (Fletcher et al., 2010, 2013), from which we had drawn to parameterize the baseline and NPP models. The harrier (NPP + HH) model corrected these departures during the first half of the study when numbers of buzzards were low but, as buzzard numbers increased, the harrier model too produced predictions that were unduly optimistic; the buzzard model, which combined the effects of non-protected predator control, hen harriers, and buzzards, corrected the overshoot. Adding a habitat effect to the buzzard model produced a small but generally consistent underprediction (Figure 5).

We did not find evidence to suggest that using the independent Otterburn/Norway data for the baseline and NPP models and Langholm data for more complex models influenced the outcomes. We used non-Langholm data for the core modeling to avoid the risk of circularity, but in essence the baseline model is a simple exponential (summer) coupled with a logistic (winter), and the NPP model is a two-level exponential (summer) coupled with a logistic (winter), with added noise generated by weather and worms. The observed changes in grouse density were too complex to be explained by even vertically shifted predictions from the baseline and NPP models, and it was the deviations from these simple patterns that drove the outcomes and led to the more complex models being upweighted.

## Implications for red grouse population dynamics

There are several consequences of these results in terms of the importance of the different factors that could potentially influence numbers of grouse at Langholm during the study. We provide these interpretations with the understanding that all models are a simplification of reality, and that the results from our modeling exercise depend on the assumptions that we detail in the descriptions of the competing models:

1. The weight of evidence favored the most complicated models over the simpler ones, indicating that Langholm Moor provided a complex environment for red grouse, so that the numbers at any one time were the outcome of multiple factors acting in concert. Previous research at Langholm Moor has suggested that red grouse populations were affected by complex predator dynamics (Francksen et al., 2019; Ludwig, Roos, & Baines, 2020; Thirgood, Redpath, Rothery, & Aebischer, 2000), grazing dynamics (Ludwig, Aebischer, Richardson, et al., 2020; Thirgood, Redpath, Haydon, et al., 2000), and control of non-protected predators (Baines et al., 2008; Ludwig et al., 2017). Our work represents the first attempt to assess the relative strength of each factor (but please refer to New et al., 2009 for data from 1975 to 1992).

2. The decision-making context for red grouse management at Langholm was made more challenging by "messy" management, the fact that different factors took effect at different times during the study (Figure 1). However, ultimately it was this temporal disparity that allowed the weight of evidence to shift in favor of the buzzard (NPP + HH + buzzard) model. The study lasted for 28 years, and it was only over such a timeframe that the relative importance of the factors that we considered could be assessed. For instance, at low buzzard annual densities (pre-2000) the harrier and buzzard models were indistinguishable, as were their respective Bayesian weights, and it took until 2008, when buzzard densities became high, for the harrier model to be downweighted and the buzzard model to be upweighted (Figure 6). Our assessment used an a posteriori approach, which allowed us to propose models with factors that had merit during the entire 28-year study. In contrast with the support we found for the influence of buzzards on red grouse population levels, an early assessment of the effects of raptors on red grouse at Langholm Moor did not mention buzzards (Thirgood, Redpath, Rothery, & Aebischer, 2000). In fact, our results agreed with Thirgood, Redpath, Rothery, and Aebischer (2000) in that useful model predictions of red grouse populations during the early portion of the 28-year study are possible without considering the effects of buzzards; it was later in the study, when buzzard numbers increased, that models without the effect of buzzards became less effective (Figures 4, 5 and 6; Appendix S1: Figures S1–S6). Top-down limitation of prey species, such as red grouse, by predators raises complex management questions especially when predators are protected (Graham et al., 2005).

3. Indeed, the role of buzzards in this ecological system had been ambiguous prior to our study. Field work during the first part of the study (Thirgood, Redpath, Rothery, & Aebischer, 2000) had demonstrated the impact of hen harriers on red grouse. However, buzzards will scavenge kills made by other predators and fieldwork was unable to distinguish whether the grouse consumed by buzzards had been killed by them

or been scavenged from kills by other predators (Francksen et al., 2019). Our buzzard (NPP + HH + buzzard) model sought to test the hypothesis that buzzards were agents of grouse mortality by assuming that buzzards killed all grouse that they consumed (quantified in Francksen et al., 2019). By contrast, the harrier model, which included no buzzard effect, was equivalent to assuming that all grouse consumed by buzzards were scavenged. The harrier (NPP + HH) model was unequivocally downgraded as buzzards became numerous due to the overprediction of grouse numbers, despite accounting for the control of non-protected predators and the impact of harriers. Conversely, the relative evidence for the two models containing a buzzard effect increased (with biannual assessments, for instance, by the post-breeding assessment in 2018 the combined weight of the two buzzard models was 0.88 versus 0.11 for the model with harrier effects only), which strongly favors the killing hypothesis over the scavenging one.

4. The inclusion of habitat as a factor limiting pre-breeding grouse density in three out of the seven models in each model set tested the hypothesis that habitat, either on its own (baseline + habitat model) or in combination with other factors (non-protected predator + habitat model, buzzard + habitat model), was an important determinant of grouse numbers in the counted areas during the period of the study. Heather cover at Langholm fell by a third between 1997 and 2009 before starting to recover (Ludwig, Aebischer, Richardson, et al., 2020; Figure 3a), and superficially the counts of red grouse during the long-term study (Figure 1) appeared to follow the same pattern. However, the two simple habitat models (baseline + habitat, NPP + habitat) were rapidly down-weighted in the model comparison process across all three model sets (Figure 6). The more complex buzzard + habitat model initially did as well as, or better than, the buzzard model, but by the end of the first non-keepered phase relative evidence for this complex habitat model dropped below that for the buzzard model. Habitat was unusual as a competing factor in our modeling process, as the decline and subsequent restoration of heather followed an assumed smooth trend between assessment years, and it is possible that habitat loss occurred in a more punctuated or non-linear fashion between them than we assumed (Ludwig, Aebischer, Richardson, et al., 2020). Nevertheless we would have expected that any effect of habitat would be most marked during the years when relative carrying capacity was at its lowest, in 2006–2009 (Figure 3a). The buzzard + habitat model often predicted counts that were less than the actual counts (Figure 5) during this period.

Therefore, the habitat model underperformed relative to the buzzard model in the years when the effects of buzzards were becoming manifest. We conclude that across the three habitat models in our modeling framework, the addition of habitat effects usually caused predictions that were lower than similar models without the habitat effect. As such, there was no discernible value of adding the habitat effect to the top model, which included baseline, non-protected predator, hen harrier, and buzzard effects. At other temporal and spatial scales, however, there were habitat quantity thresholds associated with declines in grouse abundance (Ludwig, Aebischer, Richardson, et al., 2020), and the modeling outcome may well have been different if habitat quantity had continued to drop instead of being reversed through heather restoration management.

## Monitoring and long-term data benefits

Lindenmayer et al. (2012) suggested the multiple benefits of long-term data in ecological studies including (1) quantifying ecological responses to drivers of system change, (2) understanding complex ecosystem processes, (3) providing empirical data for use in ecological models, and (4) providing information at scales relevant to management. We believe the long-term study at Langholm supports each of these claims. Certainly, the patterns we observed in model weighting (Figure 6) suggested little evidence for simple explanations of red grouse dynamics at Langholm. However, we showed the need to include a variety of predator dynamics in a predictive model for red grouse beyond the basic factors of parasitism, shooting, and weather that were present in the baseline model. Robust management of grouse moors, therefore, necessitates assessing a suite of measures provided through a monitoring program.

The use of long-term data in a modeling framework for red grouse at Langholm has the additional advantage of reducing uncertainty about the ecological drivers in the system through the use of temporal controls when spatial controls were not available. Indeed, the assessment of drivers in our system was complicated by the highly non-experimental nature of application of management treatments (Figure 1), which is similar to real-life wildlife management on public and private lands (Johnson, 2002). Our model weights, over a period of 5 years after 1992, were able to separate competing models into a set of models with little evidence and a set of models with high support. However, an additional 15 years of monitoring was needed before the support for the most critical factors became clear. This is a marked illustration of the value of continuous long-term

monitoring (Hayes & Schradin, 2017; Hughes et al., 2017; Lindenmayer et al., 2012).

Our model set included more models than other similar Bayesian, a posteriori model-weighting exercises (Dunham & Grand, 2017; McGowan, 2015; Robinson et al., 2017). Our approach was relatively straightforward (Powell et al., 2011) and mirrored that of other assessments that have been designed to feed information directly to management (e.g., Nichols et al., 2015). The use of more complex integrated population models serves as an additional avenue for similar demographic investigations (Arnold et al., 2018; Saunders et al., 2018). Regardless of modeling framework, the availability of monitoring data is critical for assessment, noting the importance of monitoring at a frequency in keeping with the life-cycle of the monitored species, with data collection timed after critical stages in that cycle (in our case, pre- and post-breeding). We propose that managers consider the benefits and costs of monitoring with specific objectives in mind (Witmer, 2005). Our study site was not continental or regional in scope, so small enough that we were usually able to monitor it twice per year. Doing so made it possible to evaluate the demographic role of summer and winter survival separately (Ludwig, Aebischer, Bubb, Roos, & Baines, 2018); from an adaptive management viewpoint, using biannual survey data reduced the amount of variation in model predictions, although our results suggested that a single survey pre- or post-breeding would have sufficed. However, the small number of gaps in our data underscored the difficulties of maintaining monitoring schemes over long periods of time (Caughlan & Oakley, 2001), not least because of unforeseeable events such as, in our case, access restrictions due to a national outbreak of foot-and-mouth disease.

# CONCLUSION

Our study leverages the twice-annual monitoring counts for red grouse over 28 years at Langholm Moor. The complexity of the ecological system was reflected in our model comparisons, as our top model contained effects of weather, shooting, control of non-protected predators, and population levels of hen harriers and buzzards. Our model predictions were not improved through the inclusion of a habitat variable representing heather loss, suggesting that the relative role of habitat quantity, over the time-scale of this study, was not important in determining grouse abundance. Furthermore, we were able to shed light on an unresolved ecological question concerning the role of buzzards in the system: the best predictive model was the one with buzzards as an active grouse predator, providing strong probabilistic evidence against the notion that buzzards were merely scavengers. Our study may contain inferences that extend beyond our local area, but we encourage replication of this work (Johnson, 2002) at other locations. We also recommend using our adaptive modeling approach with annual monitoring for other species, especially ones with a complex interplay of factors including protected predators that is difficult to manipulate experimentally.

## CONFLICT OF INTEREST
Much of the GWCT funding for data collection for the long-term project involved charitable donations from owners of grouse moors, several of whom also pay membership subscriptions to GWCT.

## DATA AVAILABILITY STATEMENT
Data (Powell et al., 2022) are available in the UNL Data Repository at https://doi.org/10.32873/unl.dr.20220307

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