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RESEARCH

Occupancy and relative abundances of introduced ungulates on New Zealand's public conservation land 2012–2018

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Abstract: Introduced ungulates are an important management issue on New Zealand's public conservation land (PCL). Ungulates are harvested by recreational and commercial hunters, with some government-funded culling. A robust monitoring system is needed to reliably report trends in occupancy and abundance, and to evaluate management effectiveness. We first describe the design and implementation of a monitoring programme enabling ungulate occupancy and relative abundances to be estimated on New Zealand's PCL. Monitoring sites are located at the vertices of an 8-km grid superimposed over PCL on North, South and Stewart/Rakiura islands (i.e. a spatially representative sampling network). At each site, intact ungulate pellets are counted on four transects radiating from a 400 m^2 vegetation plot, with each 150 m transect containing 30 1-m radius plots. We next report an analysis of the first such data collected at 1346 sites during 2012–2018. Nationally, ungulate occupancy and abundance were higher at woody than at non-woody sites, and overall were higher in the North Island than in the South Island. Occupancy odds increased by 34% and 21% per annum in the North Island and South Island, respectively. Abundance (conditional on sites being occupied) increased 11% annually in the North Island, but did not change in the South Island. These increases in occupancy and abundance indicate that ungulate populations are recovering from the lows of the 1980s, likely due to reduction in both commercial harvesting and government-funded control. The data from the monitoring reported here establish a baseline against which future estimates of ungulate occupancy-abundance, and the effectiveness of management activities, can be assessed. Five-yearly remeasurements at the sites, coupled with more comprehensive recording of information on government control and commercial/recreational harvesting activities, should enable the drivers of future changes in ungulate occupancy and abundance to be better understood.

Keywords: commercial harvesting, deer, Department of Conservation, faecal pellet index, hurdle model, North Island, recreational hunting, red deer, South Island, Stewart Island

Introduction

Browsing mammals were absent from New Zealand prior to the arrival of Europeans, who introduced many species. Now, there are wild populations of 14 ungulate taxa in New Zealand (King & Forsyth 2021; Table 1). There is concern about the impacts of these ungulates on New Zealand's ecosystems (Holloway 1950; Veblen & Stewart 1982; Wardle 1984; Nugent et al. 2001; Wardle et al. 2001; Forsyth et al. 2010), with large-scale government-funded ground- and helicopter-based hunting implemented in the past to control many populations (Caughley 1983; Harris 2002). There has also been a long history of these

taxa being harvested for recreational and commercial purposes (Caughley 1983; Challies 1985; Challies 1991; Nugent 1992; Nugent & Fraser 1993). Consequently, there is substantial interest in understanding the spatial and temporal trends in the abundances of ungulates, and how government control and recreational and commercial harvesting are affecting them.

The Department of Conservation (DOC) manages approximately one-third of New Zealand's land area (termed public conservation land; PCL), with a mandate to conserve its natural heritage values. This mandate requires DOC to know when natural heritage outcomes are being achieved and how management interventions can be used to improve

Table 1. The 11 ungulate species including in the monitoring reported here (i.e. their pellets are indistinguishable in the field) and their distribution on public conservation land (PCL) in the North Island (NI), South Island (SI) and Stewart Island/Rakiura (St/R). Three other species, feral pig (*Sus scrofa*), feral horse (*Equus caballus*) and feral cattle (*Bos taurus*) also occur on PCL, but are not considered here because their faecal pellets are easily distinguished from the 11 tabulated species. Moose (*Alces alces*) are either extinct, or nearly so, and are not included. For more information on these taxa, including the most recent distribution maps, see King and Forsyth (2021).

Species		Distribution
Western red deer	*Cervus elaphus*	NI, SI, St/R
Wapiti[a]	*Cervus canadensis*	SI
Sika deer	*Cervus nippon*	NI
Rusa deer	*Rusa timorensis*	NI
Sambar deer	*Rusa unicolor*	NI
Common fallow deer	*Dama dama*	NI, SI
White-tailed deer	*Odocoileus virginianus*	SI, St/R
Feral goat	*Capra hircus*	NI, SI
Alpine chamois	*Rupicapra rupicapra*	SI
Himalayan tahr	*Hemitragus jemlahicus*	SI
Feral sheep	*Ovis aries*	NI, SI

[a]Wapiti on PCL are hybrids with western red deer, and were indistinguishable using our faecal DNA test.

poor outcomes. Introduced ungulates are widespread on PCL, except in Northland where there has been a strategy of eradicating new ungulate populations (Fraser et al. 2003), and hence ungulate management (including management of recreational and commercial harvesters) is an important function of DOC (Parkes & Murphy 2003). Historically, there has been substantial locally motivated monitoring of ungulate abundances on New Zealand's conservation land, mostly using faecal pellet counts as indices of abundance (Baddeley 1985; Forsyth et al. 2011). These monitoring programmes have seldom been sustained, however, and much of the data collected in them have been lost (Forsyth et al. 2011). To provide a more rigorous approach to reporting on the effectiveness of its biodiversity management, DOC has developed a Biodiversity Assessment Framework (BAF; Lee et al. 2005) and Biodiversity Monitoring and Reporting System (BMRS; Department of Conservation 2020). McGlone et al. (2020) discuss the BAF—its structure, high-level goals, and broad objectives, and how they relate to the underpinning concepts of ecological integrity and ecosystem health. The BAF outlines what data are needed, but it is not a monitoring work plan. Separate monitoring programmes that can provide the data corresponding to DOC's needs are outlined by the BMRS. The Tier 1 terrestrial monitoring programme seeks to provide a national context for status and trend, using a systematic placement of sites across PCL, and it is the focus of this paper. The BMRS monitors five indicators: (1) assemblages of widespread animal species (birds), (2) distribution and abundance of exotic weeds, (3) distribution and abundance of exotic pests, (4) size-class structure of canopy dominants, and (5) functional characteristics of plant and bird communities. The data obtained enables DOC to (1) report on biodiversity status and trend, (2) prioritise resource allocation for management actions, (3) assess the effectiveness of management and policy, and (4) provide an early-warning system for biodiversity loss (Lee et al. 2005; Allen et al. 2013).

Two indicators of status and trend are occupancy and abundance (Williams et al. 2002; MacKenzie et al. 2018), and both have been suggested as essential biodiversity variables (EBVs) that could be monitored worldwide (Pereira et al. 2013). Occupancy can be defined as the proportion of sites used by a taxon, and it can be estimated from detection/non-detection data collected at those sites (MacKenzie et al. 2002, 2018). Abundance is the number of individuals present within an area of interest, but this is difficult to estimate accurately and precisely for wild animals (Williams et al. 2002). Hence, indices of relative abundance ("any measurable correlative of density"; Caughley 1977) are more commonly used as the basis for decision-making in the management of animal populations. Occupancy and abundance are inter-related, but many studies report only one quantity: jointly reporting occupancy and abundance provides a fuller assessment of status and trend (Wenger & Freeman 2008).

In this paper, we first report the design and implementation of ungulate monitoring within the BMRS. We next report key results from the first measurement cycle, including spatial and temporal trends in ungulate occupancy-abundance on PCL and the effects of government-funded management actions and commercial harvesting on ungulate occupancy-abundance. Finally, we describe the opportunities provided by this monitoring programme and discuss its limitations.

Methods

Design of the ungulate monitoring within DOC's Biodiversity Monitoring and Reporting System

The BMRS builds on the network of carbon monitoring plots established in New Zealand during the early 2000s (Payton et al. 2004) by conducting monitoring at sites located at the vertices of an 8-km grid superimposed over New Zealand's PCL, including the North Island, South Island, Stewart Island/Rakiura and near-offshore islands (Fig. 1). Since the origin of the grid was randomly selected, this is a spatially representative monitoring system. For further details on the grid, see Holdaway (2017). A 20 × 20 m permanently marked plot is located at the centroid of each site, and the vegetation structure and composition of the plot is measured (Hurst & Allen 2007a, b; Fig. 2). For more information on the BMRS, see Bellingham et al. (2020).

The technique recommended for monitoring ungulates was helicopter-based counts within 4 km² quadrats centred
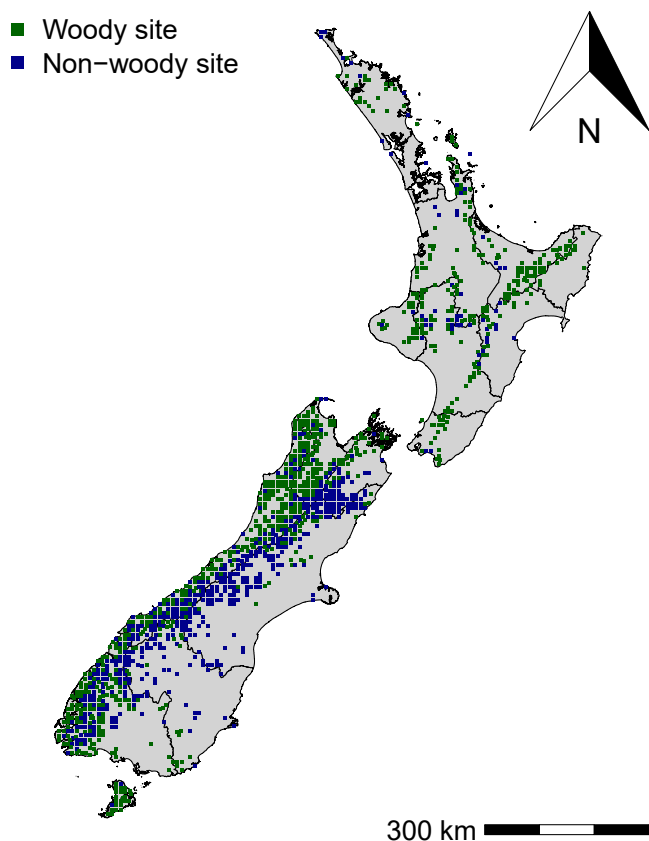
Figure 1. Locations of the 1346 sites on New Zealand's public conservation land at which ungulate monitoring occurred during 2012–2018. Each site was sampled once.
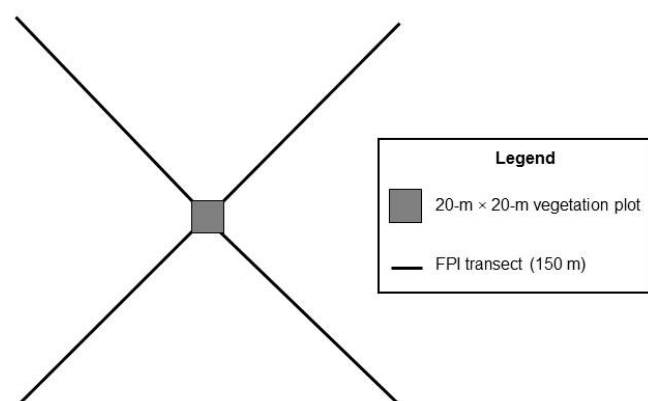
Figure 2. Spatial design of ungulate and vegetation monitoring conducted at each site. Ungulate pellets were counted along each of the four 150-m faecal pellet index (FPI) transects, following Forsyth (2005), and vegetation was measured inside the 400 m² plot, following Hurst & Allen (2007a, b).

on the vegetation plot (Allen et al. 2013), but this method was not further evaluated due to its high estimated cost. Helicopter counts within 4 km² quadrats have subsequently been used to estimate ungulate abundances at sites within the Himalayan tahr range (Ramsey & Forsyth 2019), but these are not discussed further here. A cheaper technique, counting intact ungulate pellets along transects of 30 quadrats of 1 m radius (Forsyth 2005; Forsyth et al. 2007), was therefore used. The sum of the

numbers of intact pellets counted along a transect, termed the faecal pellet index (FPI), was the variable of interest. In steep or otherwise dangerous terrain, not all quadrats on a transect can be sampled; for those quadrats, the FPI is calculated by dividing the total number of intact pellets by the number of quadrats sampled and then multiplying by 30.

Forsyth et al. (2007) showed a positive and approximately linear relationship between FPI and known deer density in 20 enclosures throughout New Zealand, and a subsequent study showed a positive curvilinear relationship between helicopter counts of ungulates (primarily feral goat) and FPI (Forsyth et al. 2014). It is therefore reasonable to infer that higher faecal pellet abundances indicate higher ungulate abundances. To increase the probability of detecting pellets at a site, four transects radiating from the four corners of the 20 × 20 m vegetation plot (Fig. 2) are monitored. For further details on the field data collection, see the Field protocols for pest mammal, bird and RECCE surveys and soil (Department of Conservation, 2012).

The faecal pellets of the seven deer taxa (Table 1), feral goat, feral sheep, alpine chamois and Himalayan tahr cannot be reliably distinguished in the field. Hence, FPI is a relative abundance index of all those taxa at a site. To determine the ungulate species present at a site we analysed faecal DNA swabbed from freshly deposited pellet groups. The faecal DNA field protocol is provided in Appendix S1 in Supplementary Materials, and the laboratory procedure is described in Ramón-Laca et al. (2014). Because faecal DNA was swabbed from fresh pellet groups, and older pellets were also included in the FPI, ungulate species were detected by faecal DNA at only a small proportion of sites at which ungulate pellets were detected. For some analyses we therefore also used the most recent ungulate distribution maps (Kappers & Smith 2009; Department of Conservation 2014) to classify sites according to the ungulate species likely to be present there.

Pilot study

The design was tested in a pilot study undertaken during the austral summer of 2008–2009. The pilot study design involved selecting six locations on the 8 × 8 km grid in each of forest, shrubland and grassland on PCL nationally. The pilot study enabled us to assess: (1) the feasibility of field measurements, (2) DOC staff time and costs, (3) improvements in sampling estimates, and (4) estimates of measures nationally for PCL. The results of the pilot study are reported in Allen et al. (2013). There were no material changes to the protocol following the pilot study.

Phased implementation of the monitoring

The ungulate measures as described above were collected at 68 randomly selected sites on the 8 × 8 km grid in forest and shrubland ecosystems (termed 'woody sites') in the 2011–2012 field season, and at 80 randomly selected sites in non-woody ecosystems ('non-woody sites') in 2012–2013. Hereinafter, field seasons spanning two calendar years are labelled as the latter year; e.g. October 2011–April 2012 (2011–2012) is '2012'. Sites were defined as woody or non-woody using the New Zealand Land Cover Database v3.0 (Land Resource Information Systems Portal 2018), checked with vegetation measures made at the site. From 2013–2014, a full annual schedule of measurement was implemented across all PCL, with approximately 20% of sites being sampled annually without replacement (i.e. sites were sampled once; Table 2).

Table 2. Numbers of sites sampled on New Zealand's public conservation land during the first cycle of measurement, from 2011–2012 to 2017–2018 (field seasons spanned October to April). Sites were randomly selected without replacement (i.e. sampled once) from the vertices of an 8 × 8 km grid (Fig. 1). Following the phased implementation in 2011–2012 and 2012–2013, approximately 20% of the total sites ($n = 1346$) were monitored annually, except in 2015–2016, when a reduced number was sampled to make up the balance of the sites already monitored during the phased implementation.

Field season	Woody sites	Non-woody sites	Total sites
2011−2012	68	0	68
2012−2013	14	80	94
2013−2014	170	116	286
2014−2015	156	110	266
2015–2016	77	28	105
2016–2017	149	109	258
2017–2018	153	116	269
Total	787	559	1346

All field sampling was conducted by purpose-recruited and -trained DOC staff.

Analyses

We first calculated naïve ungulate occupancy rates and abundance (FPI) values (i.e. not accounting for detection probability p) so that other researchers and managers can easily compare their local estimates of ungulate occupancy and/or FPI values with these data, as was done by Bellingham et al. (2016) and Whyte & Lusk (2019) for the subset of data available then. We present naïve ungulate occupancy rates and FPI values at the national (i.e. all sites shown in Fig. 1) and island (i.e. North, South and Stewart/Rakiura) scales.

We used a hurdle lognormal model in a Bayesian framework to evaluate variation in ungulate occupancy rates and FPI as a function of predictor variables. This model has two submodels: an occupancy model and a conditional abundance model (Fletcher et al. 2005). This approach enables occupancy and abundance to be modelled simultaneously and derived parameters to be estimated. The occupancy component estimates the probability that a site has ≥ 1 faecal pellet, and the conditional abundance component models the faecal pellet index (*FPI*), conditional on ≥ 1 faecal pellet being present at that site.

We first constructed a state-space occupancy model (MacKenzie et al. 2018) in a Bayesian framework (Appendix S2–S4). This model revealed that the probability of detecting ungulate pellets on one transect at a site (p) was 0.699 (95% credible interval (CI): 0.683–0.713). Since there were four transects at a site, the cumulative probability of detecting at least one pellet at a site (p^*) was therefore 0.992 (95% CI: 0.990–0.999), meaning that it was unnecessary to include imperfect detection in the occupancy submodel of the hurdle model described below.

There is wide variation in vegetation types (Wiser et al. 2011), ungulate species (Fraser et al. 2000; King & Forsyth 2021), recreational harvests (Nugent 1992; Kerr & Abell 2014), commercial harvests (D. McGregor, AsureQuality Ltd, unpubl. data), and DOC-funded control between New Zealand's three main islands. We therefore modelled ungulate occupancy and conditional abundance independently for each of these three islands within a single overall model. Site location (latitude and longitude) is correlated with many abiotic and biotic variables on PCL (Forsyth et al. 2018), so we used a two-dimensional smoother to account for site location in the occupancy and conditional abundance submodels. Two management variables were included in our analyses. The first management variable

was whether or not commercial helicopter-based wild animal recovery operations (WAROs) were permitted at a site during 2012–2018. We emphasise that WARO permission does not mean that this activity occurred at a site: unfortunately, WARO activity data (i.e. hunting effort and harvest by date and place) are not collected by DOC. However, due to wild venison processing regulations (Warburton et al. 2018), we are confident that WAROs did not occur at sites at which it was not permitted. The second management variable was whether or not DOC-funded helicopter shooting of ungulates occurred either annually or every second year at a site during 2012–2018. There were sufficient sites with 'sustained aerial control' for this variable to be included only for the South Island. We wanted to include DOC-funded ground shooting as another management variable, but DOC's records of this activity were insufficiently detailed for this purpose.

Ungulates are widely considered to be more vulnerable to harvesting and control activities in non-woody habitats than in woody habitats. For example, WAROs reduced red deer densities substantially more in alpine grasslands than in forests in the southern South Island (Challies 1977; Challies 1985; Nugent et al. 1987; Warburton et al. 2018). Also, some ungulate species seem to prefer woody habitat (e.g. rusa deer and sambar deer, both present only in the North Island; Allen 2021; Nugent 2021a), but others prefer non-woody habitat (e.g. Himalayan tahr; Forsyth & Tustin 2021). We therefore included whether a site was dominated by woody or non-woody vegetation as a variable in the occupancy model.

Many ungulate species in New Zealand have expanded their ranges in recent decades (Fraser et al. 2000; King & Forsyth 2021) and/or are thought to be recovering from the intensive harvesting and/or government-funded control that reduced ungulates to low densities in the 1980s (Forsyth et al. 2011; Warburton et al. 2018; Forsyth & Tustin 2021). It is therefore possible that ungulate occupancy and/or abundance could have increased in the seven years of monitoring (2012–2018). Since sites were randomly selected (without replacement) for sampling each year, temporal changes in occupancy and/or conditional abundance would be independent of site selection. We therefore included year as an explanatory variable in both submodels. The hurdle lognormal was:

$$Z_i \sim Bernoulli(\eta_i) \tag{1}$$

$$\text{logit}(\eta_i) = s_1\,(Location_i) + \alpha_j + \beta_{1,j}\,Year_i + \beta_{2,j}\,Woody_i + \beta_{3,j}\,WARO_i + \beta_{4,j}\,SAC_i \tag{2}$$

$$FPI_i|z_{i=1} \sim LN(\mu_i, \sigma^2) \tag{3}$$

$$\mu_i = s_2\,(Location_i) + \gamma_j + \delta_{1,j}\,Year_i + \delta_{2,j}\,WARO_i + \delta_{3,j}\,SAC_i \tag{4}$$

where Z_i is one if site i is occupied and zero otherwise; η_i is the occupancy rate for a site like i; $Location_i$ is the coordinates of plot i in New Zealand Transverse Mercator 2000; j is the island (North, South or Stewart/Rakiura) on which site i is located; $WARO_i$ is one if site i is gazetted as available for WAROs and zero otherwise; SAC_i is one if the area is subject to sustained ungulate control and zero otherwise; FPI_i is the ungulate FPI at site i. The location variables have tensor product smoothers, indicated by the functions s_1 and s_2, and used North, South and Stewart Island/Rakiura as factors to prevent locations close to one another but on different islands from influencing one another. Occupancy was modelled on the logit scale, so we used the change in odds when discussing the effects of predictor variables on occupancy rate because this metric does not rely on the underlying occupancy rate at that time or place (for further explanation, see Appendix S5).

Red deer and their wapiti hybrids have been almost exclusively the target of WAROs on PCL during 2012–2018 and in the preceding decade (Nugent & Forsyth 2021; Latham & Nugent 2021). We therefore conducted an additional analysis of sites in each of the North and South Islands where red deer rather than other ungulates are likely to be numerically dominant. In particular, feral goat (North and South Islands) and Himalayan tahr (South Island) have either excluded red deer and/or commonly attained much higher densities than red deer in recent decades (Forsyth and Hickling 1998; Forsyth et al. 2014; Parkes 2021), and hence they could potentially obscure significant impacts of WAROs on red deer occupancy-abundance. We therefore used the current ungulate distribution GIS layers (Department of Conservation 2014) to identify the North Island and South Island sites with red deer but not feral goat or Himalayan tahr.

All analyses were conducted using the statistical software program R (R Core Team 2019). The Bayesian occupancy models were constructed in JAGS (Plummer 2003) using the package R2jags (Su & Yajima, 2015). The Bayesian hurdle lognormal model was constructed in STAN using the package brms (Bürkner 2017). The Bayesian models used uninformative priors for all parameters (Appendix S6). STAN uses no u-turn sampling (NUTS), which is more efficient than Metropolis or Gibbs sampling (Hoffman & Gelman 2014). Hence, four chains were run through 2000 iterations with a 1000 iteration burn-in and no thinning. For all analyses, trace plots for each parameter in the models indicated that the Markov chains were well mixed. All parameters had Gelman-Rubin statistic values of < 1.005, indicating convergence of the chains and reliable samples for posterior inference (Gelman & Rubin 1992). We assessed the fit of our Bayesian models using Bayesian R^2 values (Gelman et al. 2019).

Results

During the seven field seasons 2012–2018, a total of 1346 sites were sampled (Table 2). There were 316 sites sampled on North Island (and near-offshore islands), 1005 sites on South Island (and near-offshore islands in the Marlborough Sounds), and 25 sites on Stewart Island/Rakiura. Due to dangerous terrain or other barriers, the full 120 quadrats (30 on each of 4 transects) could not be sampled at 260 of the 1346 sites.

Faecal DNA detected nine of the 11 taxa considered to be present on PCL during 2012–2018 (Table 3). Sambar deer, which have a restricted distribution on PCL in the North Island (Nugent 2021), were not detected. All 'wapiti' on PCL are red deer hybrids (Latham and Nugent 2021), and could not be distinguished from the latter using our assay (Ramón-Laca et al. 2014). Of the taxa detected, red deer/wapiti were the most common taxa in the North (48 sites) and South islands (91 sites), and white-tailed deer on Stewart Island/Rakiura (6 sites). Feral goat was the second most common taxa detected in the North and South Islands. The only other taxa to be detected at > 10 sites was alpine chamois, which was detected at 12 South Island sites.

Table 3. Ungulate taxa detected by faecal DNA at sites in the North, South and Stewart islands during 2012–2018. A total of 1346 sites were sampled once. The taxa detected at the subset of sites within the most recently mapped red deer distribution but outside the most recently mapped distributions of feral goat (North and South Islands) and Himalayan tahr (South Island) are also shown. For details of the faecal DNA field and laboratory methods, see Appendix S1 and Ramón-Laca et al. (2014), respectively.

Ungulate taxa	North Island		South Island		Stewart Island/Rakiura (*n* = 25)
	All sites (*n* = 316)	Sites with red deer but no feral goat[a] (*n* = 69)	All sites (*n* = 1005)	Sites with red deer but no feral goat or Himalayan tahr[a] (*n* = 485)	
Red deer / wapiti	48	26	91	59	0
Feral goat	26	1	25	0	0
Alpine chamois	0	0	12	3	0
White-tailed deer	0	0	0	0	6
Sika deer	5	5	0	0	0
Fallow deer	0	0	3	2	0
Himalayan tahr	0	0	4	0	0
Rusa deer	1	1	0	0	0
Sheep	0	0	1	0	0
Sambar deer	0	0	0	0	0

[a]One site within the North Island red deer distribution but outside the nominal distribution of feral goat had the latter species detected there. This result highlights the uncertainty around distribution maps. No sites within the South Island red deer distribution but outside the nominal distributions of feral goat and Himalayan tahr had either of those species detected there.

Ungulate occupancy and abundance by island and in woody vs non-woody ecosystems

Naïve ungulate occupancy and abundance estimates by island and in woody versus non-woody ecosystems are tabulated and mapped in Appendix S7. Across all 1346 sites, the median estimated ungulate occupancy rate (from the posterior distribution) was notably higher (as determined by non-overlapping 95% credible intervals) for the North Island (0.772) than for the South Island (0.677) (Table 4; Fig. 3). However, ungulates were detected at only three sites north of Auckland (Appendix S7), and this was reflected in the low modelled occupancy probability for Northland (Fig. 3). Modelled occupancy rates were notably higher at woody than at non-woody sites in the North and South Islands, and hence for all PCL (Table 4; Fig. 3).

Modelled unconditional abundances exhibited similar patterns to those described for occupancy, but the 95% CIs were broader (Table 5; Fig. 4). In the North Island there were high modelled ungulate abundances in the central North Island and low modelled ungulate abundances north of Waikato (Fig. 4). In the South Island there were high modelled ungulate abundances in the north-east (Marlborough/Nelson) and low modelled ungulate abundances in the coastal north-west (Fig. 4).

Effects of time, WARO status and aerial control on ungulate occupancy and abundance

North Island

There was strong evidence that ungulate occupancy at North Island sites varied with time, WARO status and by habitat (Fig. 5a; Table 6). During the seven years of monitoring, the annual odds of detecting ungulate pellets at a site increased by 34% (95% CI: 4–72). The odds of detecting ungulate pellets at woody sites were 26 times greater (95% CI: 9–81) than at non-woody sites. The odds of detecting ungulate pellets at sites at which WAROs were permitted were 3.7 times greater (95% CI: 1.5–8.8) than at sites at which WAROs were not permitted. There was also evidence that the conditional FPI increased over time on the North Island (Fig. 5b). The average annual increase in the conditional FPI on the North Island was 11% (95% CI: 1–22). There was insufficient evidence to suggest that any other explanatory variables used in the conditional FPI model were associated with changes in the FPI.

There were 69 sites that were within the red deer distribution but outside the feral goat distribution (Table 3). At these sites, there was strong evidence that the likelihood of detecting ungulate pellets changed with time and habitat (Table 6; Fig. 7). Over the seven years of monitoring, the median

annual odds of a site being occupied increased by a factor of 1.7 (95% CI: 1.2–2.5). The odds of a site being occupied was 80 times greater (16–534) at woody sites than at non-woody sites. Ungulate occupancy rates were higher at sites where WAROs were permitted (0.97; 95% CI: 0.94–0.99) than at sites at which WAROs were not permitted (0.89; 0.83–0.93) (Table 7). Sites within the North Island red deer distribution where WAROs were permitted had a conditional FPI that was 37% (95% CI: 6–58) lower than those where WAROs were not permitted (Table 7; Fig. 7).

South Island

There was strong evidence that occupancy at South Island sites varied with time and habitat (Fig. 5a; Table 6). During the seven years of monitoring, the annual odds of a site being occupied increased by 21% (95% CI: 13–31). The odds of a site being occupied were 3.1 times greater (2.2–4.4) at woody than at non-woody sites. There was no evidence that the conditional FPI increased over time (Fig. 5b). There was also no evidence that the WARO status of a site influenced ungulate occupancy or conditional abundance (Table 6). Sustained aerial control had a negative average effect on both occupancy and conditional abundance, but the 95% CIs for both parameter estimates included zero (Table 6).

There were 485 sites that were within the red deer distribution but outside the feral goat and Himalayan tahr distributions (Table 3). For these sites, there was little difference between occupancy at sites where WAROs were (0.691; 95% CI: 0.656–0.726) and were not (0.668; 95% CI: 0.603–0.728) permitted. There was a small difference between the average estimated FPI at sites where WAROs were (53.5; 95% CI: 43.0–67.2) and were not (65.4; 95% CI: 48.2–89.6) permitted. Comparison of posterior distributions indicated that 90% of sites where WAROs were permitted had a lower average FPI than sites where WAROs were not permitted. There was strong evidence that occupancy changed with time and habitat (Table 7). The annual odds of a site being occupied increased by 20% (12–30%), and the odds of a woody site being occupied was 3.0 (2.1–4.2) times greater than the odds of a non-woody site being occupied. There was no evidence that occupancy or conditional FPI differed with WARO status or with sustained control (Table 7; Fig. 6).

Stewart Island/Rakiura

Since there were only 25 sites on this island, the inferences that can be made from these data are limited relative to the North and South Islands. However, all 25 sites on Stewart Island/Rakiura are within the white-tailed deer distribution (Department of

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Table 4. Median (95% credible interval) modelled occupancy of ungulates (i.e. estimated probability of presence of at least one intact faecal pellet) on New Zealand's public conservation land, 2012–2018. *n*, number of sites sampled. All sites were monitored once.
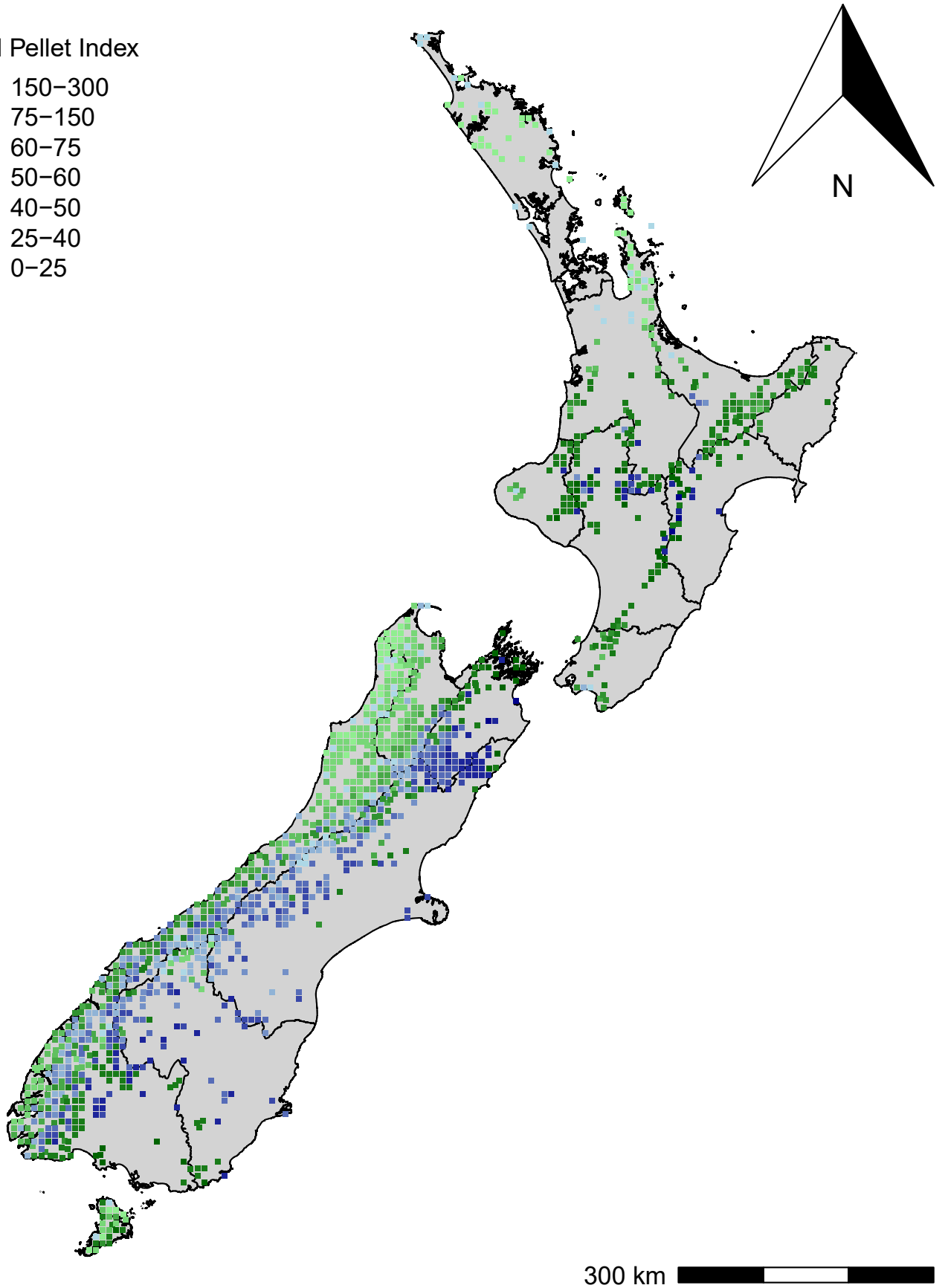
Sites	Woody	Non-woody	Total
All	0.789 (0.762–0.815) (*n* = 787)	0.573 (0.533–0.612) (*n* = 559)	0.693 (0.666–0.718) (*n* = 1346)
North Island	0.817 (0.783–0.847) (*n* = 260)	0.563 (0.494–0.621) (*n* = 56)	0.772 (0.734–0.805) (*n* = 316)
South Island	0.779 (0.744–0.812) (*n* = 504)	0.574 (0.533–0.616) (*n* = 501)	0.677 (0.649–0.704) (*n* = 1005)
Stewart Island/Rakiura	0.708 (0.533–0.857) (*n* = 23)	0.401 (0.158–0.711) (*n* = 2)	0.685 (0.509–0.836) (*n* = 25)
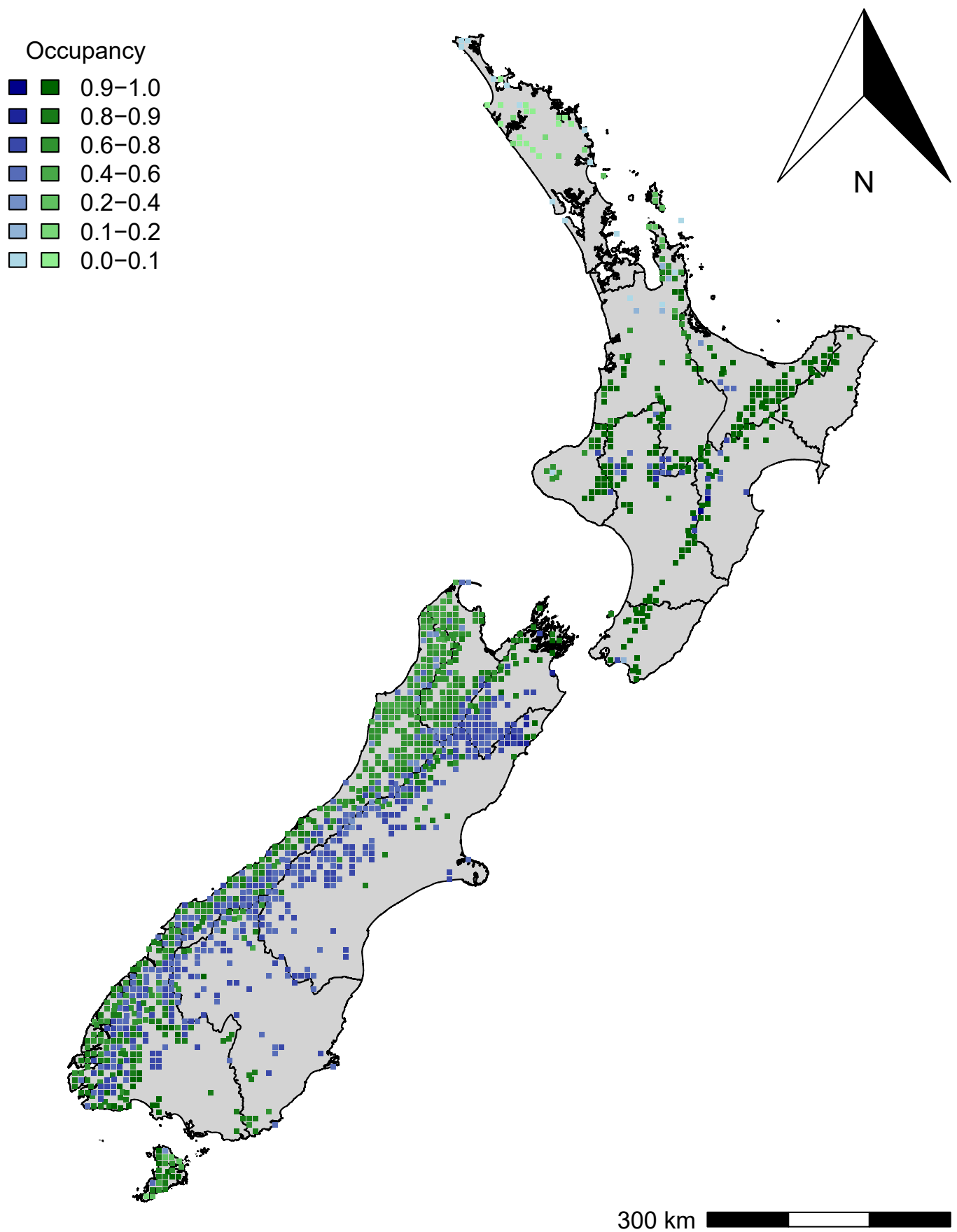
Figure 3. Modelled probability of ungulate faecal pellets being detected (occupancy) at a representative sample of 1346 sites on public conservation land, 2012–2018. Blue indicates non-woody sites; green indicates woody sites.

Figure 4. Modelled unconditional ungulate Faecal Pellet Index (FPI) at a representative sample of 1346 sites on public conservation land, 2012–2018. Blue indicates non-woody sites; green indicates woody sites.
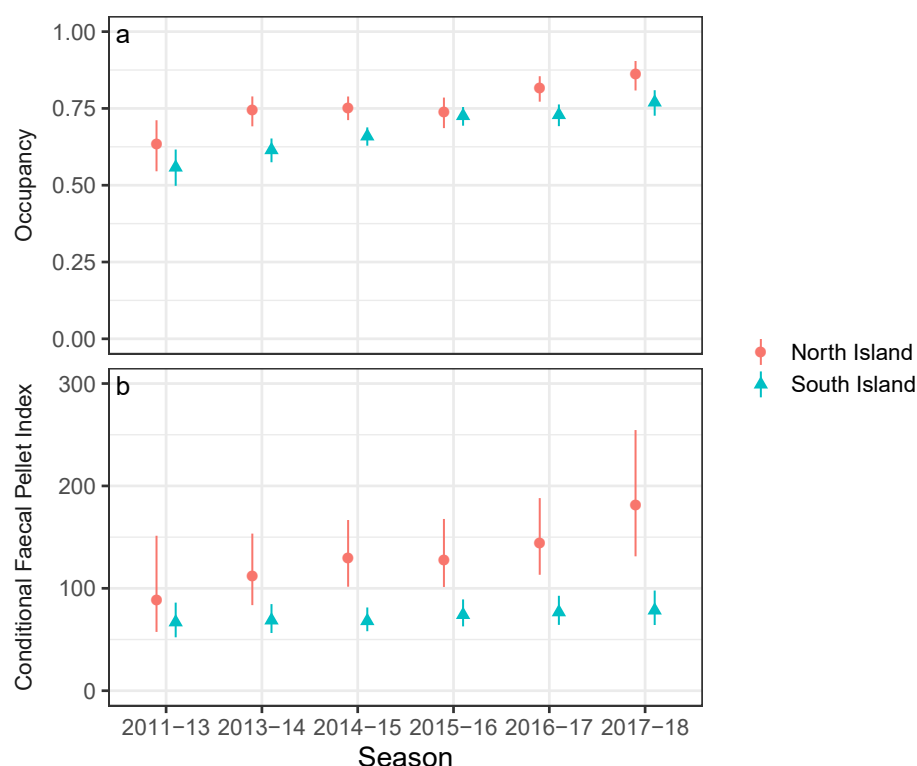
Figure 5. Temporal changes in the modelled probability of ungulate pellets being detected (occupancy) (a) and in conditional abundance (Faecal Pellet Index) (b) in the North and South Islands. Sites were sampled once. Season is the field season, each of which spanned two calendar years. Data for the first two field seasons are pooled for display due to sample size differences for woody and non-woody habitats (see Table 2).

Table 5. Median (unconditional) estimated Faecal Pellet Index (95% credible interval) of ungulates on New Zealand's public conservation land, 2012–2018. *n*, number of sites sampled. All sites were monitored once.

Sites	Woody	Non-woody	Total
All	73.0 (62.7–91.6)	53.6 (44.1–66.0)	65.3 (56.0–79.9)
	(*n* = 787)	(*n* = 559)	(*n* = 1346)
North Island	88.9 (72.1–114.0)	56.1 (38.4–81.3)	83.1 (67.2–106.8)
	(*n* = 260)	(*n* = 56)	(*n* = 316)
South Island	62.8 (51.1–79.6)	53.2 (42.9–66.5)	58.2 (47.9–71.8)
	(*n* = 504)	(*n* = 501)	(*n* = 1005)
Stewart Island/Rakiura	73.7 (34.7–566.1)	20.8 (2.6–261.7)	69.9 (33.2–549.8)
	(*n* = 23)	(*n* = 2)	(*n* = 25)

Conservation 2014). The only other ungulate present on Stewart Island/Rakiura is red deer, but this species is thought to have a restricted distribution (Department of Conservation 2014) and be uncommon relative to white-tailed deer (Nugent 2021b), a belief supported by DNA faecal sampling detecting only white-tailed deer there (Table 3). We are therefore confident in making inferences about the occupancy rates and relative abundance of white-tailed deer on Stewart Island/Rakiura. The model estimated the occupancy rate and conditional FPI on Stewart Island/Rakiura to be 0.66 (95% CI: 0.53–0.78) and 66.9 (95% CI: 33.5–512.4), respectively (Table 5). There was no evidence of a temporal change in either occupancy or unconditional FPI (Table 5). There were insufficient non-woody sites (*n* = 2) to include habitat in the model. WAROs were not permitted at any Stewart Island/Rakiura sites, and there was no sustained aerial control there.

Discussion

The monitoring programme reported here was designed to enable unbiased reporting of spatial and temporal trends in ungulate occupancy and abundance on New Zealand's PCL. The first cycle of measurements, at a representative sample of 1346 sites on PCL on the North, South and Stewart islands, provides baseline estimates of occupancy (Table 4) and relative abundance (Table 5). These measurements revealed differences in ungulate occupancy rates and abundances in relation to time, habitat and island. The effects of management (sustained aerial control and WAROs) were less clear. We emphasise that the monitoring is for all ungulates present on PCL (Table 1) except for feral cattle and feral horse (which have limited distributions and readily distinguishable faeces; Parkes 2021), and feral pig (which have a wide distribution and readily distinguishable faeces; McIlroy & Nugent 2021).

The lower ungulate occupancy rates and conditional abundances at non-woody sites likely reflects the greater vulnerability of ungulates on New Zealand's PCL to helicopter-based shooting in these habitats (deer: Challies 1977; Latham et al. 2018; Himalayan tahr: Tustin & Challies 1978). Related to this, commercial harvesting of red deer is currently more economically viable in non-woody habitats (Warburton et al. 2018). The higher occupancy rates of ungulates at woody sites in the North Island than in the South Island probably reflects

Table 6. Posterior distributions (medians and 95% credible intervals) of parameters for the ungulate occupancy-abundance model. The Bayesian R^2 for this model was 0.26. The occupancy model assumed perfect detection, and its parameters are in the logit scale. Conditional Faecal Pellet Index (FPI) parameters are in the log scale, except for standard deviation. There were insufficient North Island sites with sustained ungulate control to include this variable there. Wild animal recovery operations (WARO) were not permitted on Stewart Island/Rakiura, and no sustained ungulate control occurred there.

Island and sub-model	Parameter	Median	Lower 95% bound	Upper 95% bound
North Island				
Occupancy	Intercept	−2.05	−3.68	−0.71
Occupancy	Year	0.29	0.04	0.54
Occupancy	WARO	1.30	0.41	2.18
Occupancy	Woody	3.26	2.22	4.39
Conditional FPI	Intercept	3.16	1.92	3.94
Conditional FPI	Year	0.09	0.00	0.19
Conditional FPI	WARO	−0.32	−0.69	0.05
Conditional FPI	Standard deviation	1.26	1.16	1.38
South Island				
Occupancy	Intercept	−0.12	−0.87	0.55
Occupancy	Year	0.19	0.12	0.27
Occupancy	WARO	0.05	−0.33	0.42
Occupancy	Woody	1.13	0.79	1.49
Occupancy	Sustained control	−0.50	−1.16	0.16
Occupancy	Sustained control × woody	−0.15	−1.41	1.22
Conditional FPI	Intercept	3.12	2.52	3.70
Conditional FPI	Year	0.03	−0.04	0.09
Conditional FPI	Sustained control	−0.43	−1.00	0.15
Conditional FPI	WARO	−0.11	−0.42	0.21
Conditional FPI	Standard deviation	1.61	1.52	1.70
Stewart Island/Rakiura				
Occupancy	Intercept	−0.12	−0.87	0.55
Occupancy	Year	0.19	0.12	0.27
Conditional FPI	Intercept	3.66	2.80	4.52
Conditional FPI	Year	−0.16	−0.48	0.16
Conditional FPI	Standard deviation	1.09	0.65	1.81

Table 7. Posterior distributions (medians and 95% credible intervals) of parameters for the North Island and South Island red deer models. The Bayesian R^2 for this model was 0.23. Occupancy model parameters are in the logit scale. Conditional Faecal Pellet Index (FPI) parameters are in the log scale, except for standard deviation. There were insufficient North Island sites with sustained ungulate control to include this variable there.

Island and sub-model	Parameter	Median	Lower 95% bound	Upper 95% bound
North Island				
Occupancy	Intercept	−0.51	−2.57	1.31
Occupancy	Year	0.52	0.15	0.93
Occupancy	WARO	−0.30	−1.89	1.11
Occupancy	Woody	4.39	2.79	6.28
Conditional FPI	Intercept	3.87	3.27	4.53
Conditional FPI	Year	0.07	−0.03	0.17
Conditional FPI	WARO	−0.46	−0.86	−0.06
Conditional FPI	Standard deviation	1.27	1.16	1.40
South Island				
Occupancy	Intercept	−0.09	−0.99	0.66
Occupancy	Year	0.18	0.11	0.26
Occupancy	WARO	−0.09	−0.48	0.31
Occupancy	Woody	1.09	0.74	1.43
Occupancy	Sustained control	−0.46	−1.15	0.21
Occupancy	Sustained control × woody	−0.32	−1.59	1.08
Conditional FPI	Intercept	3.10	2.50	3.72
Conditional FPI	Year	0.04	−0.03	0.10
Conditional FPI	Sustained control	−0.43	−0.99	0.14
Conditional FPI	WARO	−0.09	−0.42	0.25
Conditional FPI	Standard deviation	1.58	1.50	1.67
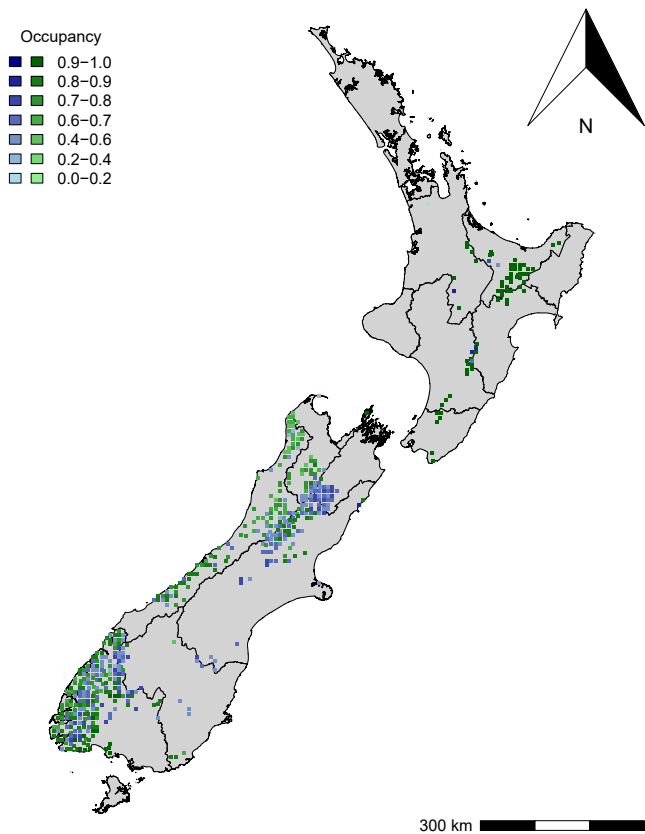
Figure 6. Modelled probability of ungulate faecal pellets being detected (occupancy) at a representative sample of sites within the distribution of red deer but not of feral goat or Himalayan tahr in the North Island (*n* = 69) and South Island (*n* = 485), 2012–2018. Blue indicates non-woody sites; green indicates woody sites.
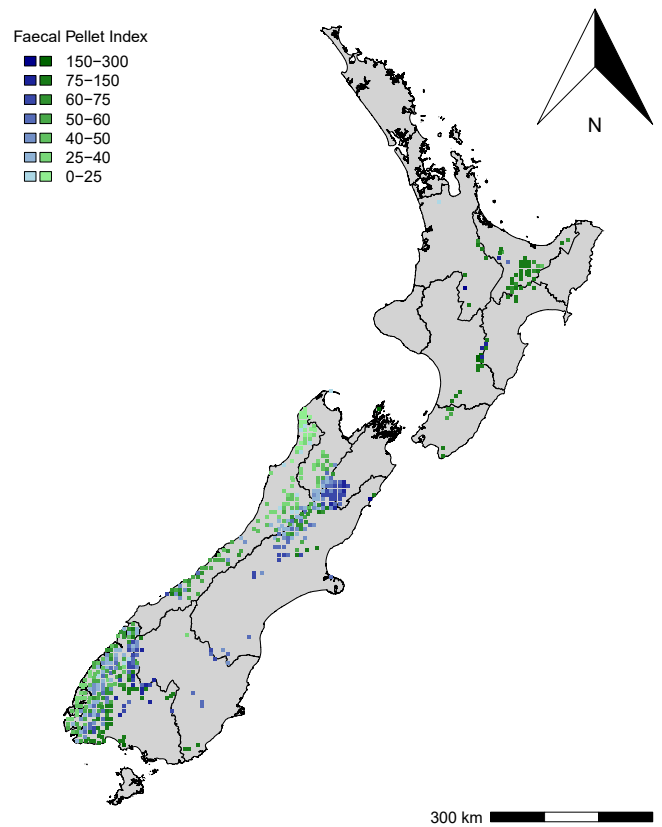
Figure 7. Modelled ungulate Faecal Pellet Index (FPI) at a representative sample of sites within the distribution of red deer but not of feral goat or Himalayan tahr in the North Island (*n* = 69) and South Island (*n* = 485), 2012–2018. Blue indicates non-woody sites; green indicates woody sites.

several factors: first, the greater diversity of forest-dwelling ungulates in the North Island, e.g. sika deer, sambar deer and rusa deer are present only in the North Island; second, red deer is the most widespread ungulate species in South Island forests, and in the last decade there has been a substantially larger commercial harvest of red deer in the South Island than in the North Island (D. McGregor, AsureQuality Ltd, unpubl. data). The higher occupancy rate in South Island non-woody sites is likely to be at least partly a consequence of two alpine ungulates, Himalayan tahr and alpine chamois, being present there. The latter's distribution includes most of the South Island PCL above the tree-line (Forsyth 2021). Himalayan tahr have a more limited distribution, but have locally high densities (Ramsey & Forsyth 2019; Forsyth & Tustin 2021).

Ungulate occupancy rate odds increased at similar rates in the North and South Islands (34% and 21% per annum, respectively) over the period 2012–2018. The most important driver of these increases is likely to be reduced harvests allowing ungulate populations to increase from the low densities of the 1980s (Forsyth et al. 2011; Warburton et al. 2018; Nugent & Forsyth 2021). The key harvesters of ungulates in New Zealand are (in descending qualitative order of harvest size) recreational harvesters (Nugent 1992; Warburton et al. 2018; Nugent & Forsyth 2021), commercial harvesters and DOC-funded culling. There have not been any robust estimates of recreational hunter harvests since 1988 (Nugent 1992; Warburton et al. 2018), and DOC-funded culling data have not

been systematically collated for all PCL. There are, however, robust records of the numbers of wild ungulates that have been harvested and inspected prior to processing for human consumption, and these data indicate that the numbers of deer harvested declined sharply in the 2000s before increasing again in the 2010s (Nugent & Forsyth 2021). Whereas all species of deer, plus Himalayan tahr and alpine chamois, were harvested in the 1970s and 1980s, now only red deer and their wapiti hybrids are harvested (Nugent & Forsyth 2021; Latham & Nugent 2021). The lower commercial harvests, reduced to zero for many species, reflect reduced profitability due to lower real prices per animal harvested and higher operating and compliance costs (Parkes & Murphy 2003; Nugent & Choquenot 2004; Parkes 2006; Warburton et al. 2018). Commercial harvesting reduced many ungulate populations from their peak densities of the 1960s and early 1970s to lows in the 1980s (deer: Nugent et al. 1987; Forsyth et al. 2011; Himalayan tahr: Forsyth & Hickling 1998), and WAROs are thought to remain a key determinant of the abundance and density of red deer over most of its South Island PCL range (Nugent & Choquenot 2004; Warburton et al. 2018; Nugent & Forsyth 2021). These temporal increases in ungulate occupancy fit with long-term faecal presence-absence data showing that ungulate abundances were at their highest in the 1950s–1970s, lower during the 1980s–1990s, but then increased (Forsyth et al. 2011). The observed increases are also consistent with the general prediction, based on bioeconomic modelling of

current commercial red deer harvesting, that "deer numbers will increase significantly" (Warburton et al. 2018). Periodic mapping of ungulate species distributions indicates that the geographic ranges of some species have increased since the mid-1990s (Fraser et al. 2000). In particular, there have been substantial increases in the distributions of red deer, fallow deer and Himalayan tahr (Nugent & Forsyth 2021; Nugent & Asher 2021; Forsyth & Tustin 2021), and a minor increase in the distribution of sambar deer (Chalmers 2018; Nugent 2021a).

Red deer have been the almost exclusive target of commercial harvesters for many years. The effects of WARO status (i.e. permitted or not) on ungulate occupancy-abundance within the parts of red deer distribution that did not overlap the distributions of feral goat and Himalayan tahr (two taxa that attain high densities) varied with metric and island. There was no evidence of an effect of WARO status on red deer occupancy in the North or South island, but conditional abundance was on average 37% lower at North Island sites where WAROs were permitted than at sites where WAROs were not permitted. There was no effect of WARO status on conditional abundance in the South Island. This island difference most likely arises from different harvesting intensities in the two islands, but without WARO harvest effort and kill data this relationship cannot be further evaluated.

The effects of sustained DOC-funded aerial control on ungulate occupancy and conditional abundance was only evaluated for the South Island. Sustained aerial control did have, on average, negative effects on ungulate occupancy and conditional abundance, but the effect was too variable to be considered significant. An experiment conducted in two North Island forests and one South Island forest during 2003–2011 (i.e. prior to the monitoring reported here) also revealed a negative relationship between helicopter-based shooting effort and ungulate FPI, again with large uncertainty (Forsyth et al. 2013). Hence, although sustained helicopter-based shooting can reduce ungulate densities, it does not always seem to be the case in forests, where ungulates are more difficult to detect from a helicopter (see above).

The near-absence of ungulate pellets detected on PCL north of Auckland is consistent with other knowledge about the low occupancy of ungulates there (Fraser et al. 2000, 2003). This finding suggests that the long-term strategy of eradicating new populations of ungulates that are detected in Northland (Fraser et al. 2003) has been mostly successful. The detection of pellets at three Northland sites (Appendix S7) is a warning that this strategy needs to be ongoing and sufficiently funded if that area is be kept ungulate-free.

Opportunities provided by this monitoring programme

The BMRS sites reported here are being remeasured on a five-year rotation (EFW, unpubl. data), as was proposed in the original design (Allen et al. 2013). Those repeated measurements should enable the effects of management on ungulate occupancy rates and abundances to be better estimated, because occupancy-abundance at t_1 can be included in analyses. (Repeat measures from the same sites are more powerful than measurements from new sites, because inter-site variability is reduced.) Hence, temporal changes in ungulate occupancy rates and abundances will be able to be updated, using data from all 1346 sites, after the 2022–2023 field season. Detections of ungulate species at sites by their faecal DNA (Table 3) can be used to determine range expansions at multiple scales including region (e.g. into Northland) and island, and to update existing range maps.

The ungulate occupancy-abundance data collected in the BMRS could be used to help select similar sites for inclusion in studies testing hypotheses about the effects of ungulate management (e.g. recreational hunting, WAROs, DOC-funded control) on ungulate abundances and impacts (e.g. Bellingham et al. 2016; Ramsey et al. 2017). We provide the naïve occupancy rates and FPI values (Appendix S7–9) to help other researchers place their smaller-scale results in a larger-scale context (e.g. see Whyte & Lusk 2019).

Vegetation, native and non-native birds, and other non-native mammals, including brushtail possums (*Trichosurus vulpecula*) and lagomorphs, are also being monitored at the 1346 sites on PCL (Bellingham et al. 2020). The ungulate occupancy and abundance data reported here can be used to test hypotheses about interactions between ungulates and these other EBVs (see Fig. 1 in Bellingham et al. 2020).

Finally, extending the monitoring programme reported here to all non-public conservation land (which is the majority of New Zealand) would enable unbiased national (i.e. all of New Zealand) reporting of ungulate status and trend (Bellingham et al. 2020). There are different challenges in sampling private land on an 8 km grid, significant ones being obtaining permissions from landholders and the potential presence of domestic ungulates.

Limitations of this monitoring programme

Faecal pellet counts have been used as an index of ungulate abundance in New Zealand forest habitats since the 1950s (Riney 1957; reviews in Forsyth et al. 2003, 2011). The true abundance of pellets at a site is an index of ungulate abundance, reflecting the number of ungulates present, their defecation rates and the decay rate of pellets. Daily defecation rates have not been estimated for ungulates in New Zealand conditions, and are likely to vary with species, animal age and sex, diet and season (Forsyth et al. 2003). Decay rates of red deer faecal pellets have been estimated on PCL (Challies 1977; Hickling 1986; Nugent et al. 1987; Fraser & Burrows 2000) and could vary with rainfall and temperature (Forsyth et al. 2003). Robustly estimating defecation and decay rates for each of the ungulate species and environments sampled in this study was infeasible (Allen et al. 2013). However, we consider the positive and linear relationship observed between FPI and the known abundances of a mix of ungulate species within 20 enclosures in the North and South Islands (Forsyth et al. 2007) justified the assumption that more pellets equates, on average, to more ungulates.

The pellets of the 11 ungulate taxa listed in Table 1 could not be reliably differentiated in the field. Faecal DNA swabs were collected to enable ungulate species present at a site to be identified (Ramón-Laca et al. 2014), but because pellets need to be fresh for DNA to be retained there was species detection data only for a small subset of sites. These DNA data were, however, useful for determining which sites within the feral goat and Himalayan tahr mapped distributions did not have those species present. This enabled a more nuanced analysis of the effects of WAROs on red deer occupancy-abundance relationships. The DNA data also confirmed that white-tailed deer were the dominant ungulate species present on Stewart Island/Rakiura (Nugent 2021).

The need to understand the effectiveness of managing exotic mammals was a key driver of the design of the BMRS (Allen et al. 2013), and control history was shown to be the primary determinant of brushtail possum abundances sampled at a subset of the sites reported here (Forsyth et al. 2018).

Management history would almost certainly be one of, if not the, most important determinants of ungulate abundances on PCL. We attempted to assess the effects of WAROs and sustained aerial control on ungulate occupancy-abundance. It would have been desirable to also include recreational hunting (probably the largest harvester of ungulates on PCL), sustained ground shooting (as is done for feral goat on PCL; Forsyth et al. 2003) and aerial 1080 poisoning operations (in which ungulates can be significant by-kill; Appendix S10) as management variables. The information available for these variables, however, was limited. Improving the quality of the data available on ungulate harvesting and control (for inclusion as covariates in ungulate occupancy-abundance models) would greatly increase the value of the data collected in this monitoring programme, and likely increase the amount of variation in the data explained by models.

The monitoring programme described here enables routine reporting (*sensu* Pergl et al. 2020) of ungulate occupancy and relative abundance on New Zealand's public conservation land. The data reported in Tables 3 and 4 provide a baseline estimate of occupancy and relative abundance for introduced ungulates on New Zealand's PCL. Ungulate occupancy and abundance were higher at woody than at non-woody sites, and overall were higher in the North Island than in the South Island. Ungulate occupancy odds increased by 34% and 21% per annum in the North Island and South Island, respectively, over the period 2012–2018. The primary driver of these increases is likely to have been reduced commercial harvesting and government-funded control, which has enabled ungulate populations to recover from the lows of the 1980s. Five-yearly remeasurements of sites, coupled with more accurate information on government control (including by-kill in aerial 1080 poisoning operations) and commercial and recreational harvesting activities, should enable the drivers of future changes in ungulate occupancy and abundance to be better understood.

Data availability

The data and code used in our analyses are in Appendix S11, enabling our results to be reproduced.

Author contributions

PDM: Conceptualisation, formal analysis, software, writing – original draft. DMF: Conceptualisation, methodology, project administration, supervision, writing – original draft. DSLR: Conceptualisation, formal analysis, project administration, writing – original draft. MP: Methodology, investigation, project administration, writing – review and editing. MM: Funding acquisition, methodology, investigation, project administration, writing – review and editing. AMG: Formal analysis, methodology, writing – review and editing. BK: Data curation, writing – review and editing. EFW: Conceptualisation, funding acquisition, methodology, project administration, supervision, writing – review and editing.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Field protocol for swabbing ungulate faecal pellets for DNA.

Appendix S2. Imperfect detection model.

Appendix S3. Prior distributions used in the Bayesian occupancy model.

Appendix S4. Posterior distributions (medians and 95% credible intervals) of parameters from the Bayesian occupancy model accounting for imperfect detection.

Appendix S5. Interpretation of results from our occupancy model.

Appendix S6. Prior distributions used in the Bayesian hurdle lognormal models.

Appendix S7. Naïve ungulate occupancy rates and abundance (Faecal Pellet Index) values 2012–2018.

Appendix S8. Histograms of observed Faecal Pellet Index (FPI) values at woody (upper; $n = 787$) and non-woody (lower; $n = 559$) sites on New Zealand public conservation land sampled during 2012–2018.

Appendix S9. Mean naïve occupancy rates and Faecal Pellet Index (FPI) values for ungulates on New Zealand's public conservation land during 2012–2018.

Appendix S10. By-kill of ungulates in aerial 1080-poisoning operations.

Appendix S11. Data and code used in analyses.

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