Estimates of Himalayan Tahr (*Hemitragus jemlahicus*) Abundance in New Zealand Results from Aerial Surveys

D.S.L Ramsey and D.M. Forsyth

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Arthur Rylah Institute for Environmental Research Department of Environment, Land, Water and Planning PO Box 137 Heidelberg, Victoria 3084

Phone (03) 9450 8600 Website: www.ari.vic.gov.au

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Estimates of Himalayan Tahr (*Hemitragus* jemlahicus) abundance in New Zealand

Results from aerial surveys

¹D.S.L. Ramsey and ²D.M. Forsyth

¹Arthur Rylah Institute for Environmental Research 123 Brown Street, Heidelberg, Victoria 3084

²Vertebrate Pest Research Unit, Department of Primary Industries 1447 Forest Road, Orange, NSW, 2800

In partnership with



Arthur Rylah Institute for Environmental Research Department of Environment, Land, Water and Planning Heidelberg, Victoria

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1 Summary

Context:

The Himalayan Tahr Control Plan (Department of Conservation 1993) defines intervention densities in terms of number of tahr per km² in each of seven management units (range: <1 to 2.5 tahr per km²) and two exclusion zones (0 per km²) and sets a limit on total population abundance (10,000 animals). Prior to this study, insufficient information existed to determine whether tahr numbers in each management unit and exclusion zone exceeded these intervention densities or whether the total population abundance exceeded the limit.

Aims:

To estimate the density and abundance of Himalayan tahr on Public Conservation Land (PCL) in each of the seven management units and two exclusion zones in the Southern Alps of New Zealand.

Methods:

Aerial surveys to count tahr and other ungulates were conducted on three occasions at 66, 2 x 2 km plots located on PCL during 2016, 2017 and 2018. The repeat counts of tahr were used to estimate abundance, corrected for imperfect detection, using an *N*-mixture model for open populations (Dail & Madsen 2011). Finite sampling methods were then used to estimate the total abundance of tahr in each management unit and exclusion zone (Skalski 1994). This work updates a previous analysis that was based on data collected in 2016 and 2017 (Ramsey 2018).

Results:

- The total abundance of tahr on PCL for the period 2016 2018 was estimated to be 34,292 individuals (95% confidence interval; 24,777 47,461).
- Tahr abundances were highest in management units 3 and 4 (approximately 8,000 tahr in each), and were lowest in management unit 7 and the two exclusions zones (approximately 100 150 tahr in each).
- Average tahr density over the three years of sampling was highest in management unit 3 (9.2 tahr/km²) and lowest in exclusion zone 2 (0.06 tahr/km²).

Conclusions and implications:

- Average tahr densities exceeded the intervention densities specified in the Himalayan Tahr Control Plan in all management units and in both exclusion zones, with the exception of management unit 7.
- The estimated total population abundance of tahr on PCL clearly exceeds the limit of 10,000 animals. Moreover, the lower 95% confidence limit of the estimate of total abundance is more than double the limit of 10,000 animals.
- Further work is currently being undertaken to investigate models of the relationship between tahr abundance and habitat characteristics. Such models could provide more fine-scale resolution of the variation in tahr abundance across the PCL.

2 Introduction

Himalayan tahr (*Hemitragus jemlahicus*) were first introduced into New Zealand in 1904 and now occupy around 9600 km² of the Southern Alps (Cruz *et al.* 2017). After commercial harvesting reduced tahr populations by around 90% during the 1960's and 1970's, the population increased 6-fold following a moratorium on commercial harvesting in 1982 (Parkes 2009). Tahr are a declared wild animal under the "Wild Animal Control Act 1977", which provides provisions for the control of introduced wild animals to protect against their damaging effects on native vegetation, soils, water and other wildlife (Department of Conservation 1993). Tahr graze primarily on alpine tussock grassland (e.g. *Chionochloa* spp.) and caused widespread impacts on montane grasslands during the 1960's when their densities were high (Parkes 2009). However, impacts are still apparent at current population densities and tahr need to be controlled to lower densities to further reduce impacts on native vegetation (Cruz *et al.* 2017).

The Himalayan Tahr Control Plan (Department of Conservation 1993) defines intervention densities in terms of number of tahr per km² in each of seven management units (range: <1 to 2.5 tahr per km²) and two exclusion zones (0 per km²) (Table 1). However, insufficient monitoring data existed to estimate tahr abundances on these management units and exclusion zones. To address that knowledge gap, aerial surveys of tahr and other ungulates were conducted at 66 sites monitored as part of the national Biodiversity Monitoring and Reporting System (BMRS) (Allen *et al.* 2013) during 2016, 2017 and 2018. These data were then used to estimate the density and total abundance of Himalayan tahr on PCL in each of the seven management units and two exclusion zones. This work updates a previous analysis that was based on the subset of 38 plots that were sampled in 2016 and 2017 (Ramsey 2018). We report results only for Himalayan tahr because this was the most abundant ungulate species and is the focus of active management by the Department of Conservation. Analysis of monitoring data for other ungulate species as well as data on ungulate faecal pellet surveys will be the focus of a separate report.

3 Methods

3.1 Plot selection

The BMRS was developed to enable reporting on the status of native biodiversity and key threats (including pest animals) on New Zealand's Public Conservation Land by collecting data at plots at the vertices of an 8-km grid superimposed over New Zealand's Public Conservation Land (i.e. a spatially representative sampling network) (Allen *et al.* 2013). The origin of the grid was selected randomly. This design resulted in a total of 112 plots within PCL across the seven tahr management units and two exclusion zones (Table 1).

Monitoring is conducted at a randomly-selected 20% of plots (without replacement) annually, such that all plots will be monitored once every five years. During 2016, 16 plots were sampled. A further 22 and 28 plots were sampled in 2017 and 2018, respectively, giving a total of 66 plots for analysis (Figure 1).

Table 1. The seven management units (MUs) and two exclusion zones (EZs) defined in the Himalayan Tahr Control Plan (Department of Conservation 1993). 'Plots' is the number of 2 x 2 km plots on PCL that is expected to be sampled with aerial survey every five years (i.e., approximately 20% are sampled in each year).

Unit/zone	Name	Intervention density (abundance)	Plots
MU1	South Rakaia/Upper Rangitata	2.5 km ² (ca. 2000)	12
MU2	South Whitcombe Wanganui/Whataroa	2.0 km ² (ca. 1500)	11
MU3	Gammack/Two Thumb	2.0 km ² (ca. 3000)	16
MU4	Mount Cook/Westland National Parks Adjoining PCL on Liebig Range	<1.0 km² (ca. <500)	18
MU5	Ben Ohau	2.5 km ² (ca. 1800)	8
MU6	Landsborough	1.5 km ² (ca. 900)	10
MU7	Wills/Makarora/Hunter	<1.0 km² (ca. <100)	10
EZ 1	North Rakaia/Mathais-North Whitcombe/Hokitika/Mungo	>0	11
EZ 2	South Of The Haast to Wanaka Highway	0	16

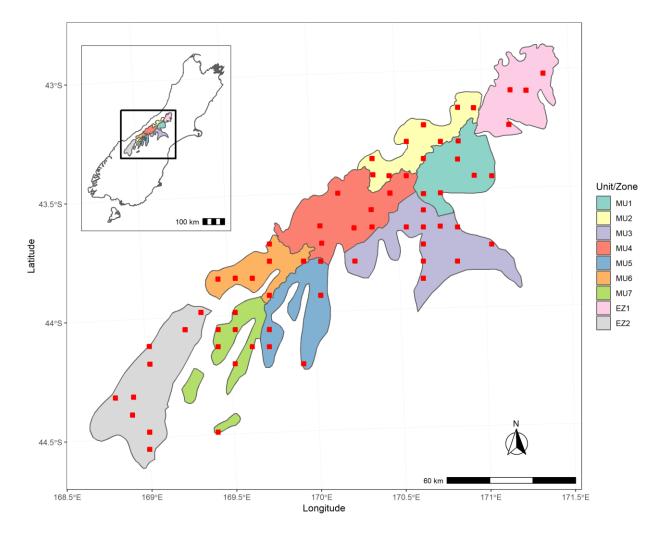


Figure 1. Location of the seven tahr management units (MU) and two exclusion zones (EZ) in the Southern Alps of New Zealand. Red squares show the locations of the 66 2 x 2 km plots where aerial surveys of tahr were undertaken.

3.2 Aerial survey protocol

The aerial survey protocol is described in detail elsewhere (Forsyth, Perry & McKay 2018 and references therein). Briefly, a 2 x 2 km plot was established at each site, with the centre of each plot being the vertex of the 8-km grid. Each 4 km² plot was subject to three separate counts undertaken from a helicopter (usually a Hughes 500D or Hughes 500E) at least 10 days apart. This interval between successive counts at a plot was chosen to minimise the disturbance effects of the helicopter on tahr in the subsequent two counts at that plot. Counts were undertaken during February—June (with most completed by May), well after the 30 November median birth date (Caughley 1971).

On each of the three sampling occasions the 4 km² plot was systematically flown by the helicopter flying at about 40–60 knots and at 20–70 m from the ground (depending on topography and wind). The pilot and one primary observer, seated next to the pilot, searched for tahr and other ungulates. When ungulates were sighted, the primary observer counted the individuals and assigned them to species (and sex-age classes where possible, but that information was not used in the analyses reported here). A recorder, seated in the rear behind the primary observer, recorded the locations and other details of each group.

3.3 Plot area

Although each plot was nominally 4 km² in area, this was the two-dimensional surface area of the plot. Due to the steep terrain on most plots, the actual surface area covered by each 4 km² area could be considerably greater than the nominal 4 km². Hence, to calculate the actual 3D surface area of each plot, each 2 x 2 km area was divided into 400 1-ha cells and the surface area of each cell calculated using a 15m digital Elevation Model (DEM). The 3D surface areas of each 1-ha cell were then added to give the 3D surface area for each plot. The 3D surface area was subsequently used for density calculations for each plot.

3.4 Abundance estimation

The total number of tahr counted within each plot, at each of the three sampling occasions, were used to estimate abundance corrected for imperfect detection using an *N*-mixture model for open populations (Dail & Madsen 2011). We assumed a simple exponential trend to model the changes in tahr abundance between successive sampling occasions (Humbert *et al.* 2009). Hence, the model was able to account for movement of tahr on or off the plot between the three sampling occasions. This model differed slightly from the model used in Ramsey (2018), which decomposed the trend between sampling occasions into survival and recruitment components. Thus, the current model has less parameters, which resulted in better numerical stability. Further details of this model are provided in Appendix 1.

For each plot, an estimate of average abundance was calculated as the mean of the estimates from the three sampling occasions. Tahr density for each plot was estimated similarly by dividing the abundance estimate by the three-dimensional area of each plot. To estimate the total abundance of tahr within each management unit / exclusion zone, we assumed that the sampled plots consisted of a stratified random sample of the total available plots that could have been sampled within each management unit, with management units forming the strata. We assumed a two-stage sampling design where the overall estimate of abundance within each unit was composed of two sources of error, the spatial variation in tahr abundance among plots within each unit and the estimation error associated with the abundance estimate for each plot. Total abundance within each management unit was then estimated as the mean plot abundance in the

unit multiplied by the total available plots within each unit. The total number of available plots within each unit was calculated by subdividing the two-dimensional area of conservation land within the unit into all possible 2 x 2 km plots. The mean tahr density for each management unit was then calculated by dividing the estimated abundance for each management unit by the two-dimensional area of the management unit. Variance of the estimates of total tahr abundance and density within each management unit and overall abundance was calculated using finite sampling methods (Skalski 1994). More details on these calculations are provided in Appendix 2.

4 Results

4.1 Tahr density and abundance

The mean density of tahr on each plot varied widely, from 0.02 to 26/km² (Figures 2 & 3). However, precision of some of the mean density estimates was low due to the changes in tahr density over the three sampling occasions at some plots (Figure A1, Appendix 3). The corresponding mean density of tahr within each management unit was also variable, ranging from 0.16/km² in MU7 to 9.17/km² in MU3 (Table 2). The mean tahr densities exceeded the intervention densities specified in the Himalayan Thar Control Plan (Table 1) in all management units except MU7. Mean tahr densities in the two exclusion zones were 0.19/km² for EZ1 and 0.06/km² for EZ2, both above the intervention density of 0 (Table 2).

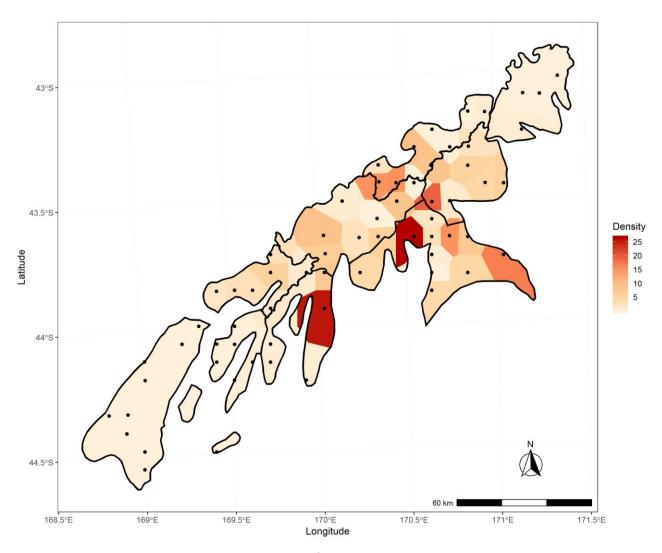


Figure 2. The average density of tahr (individuals/km²) on the area uniquely occupied by each of the 66 plots (black circles) sampled by aerial surveys during 2016, 2017 and 2018. The seven management units (MU) and two exclusion zones (EZ) are described in Table 1.

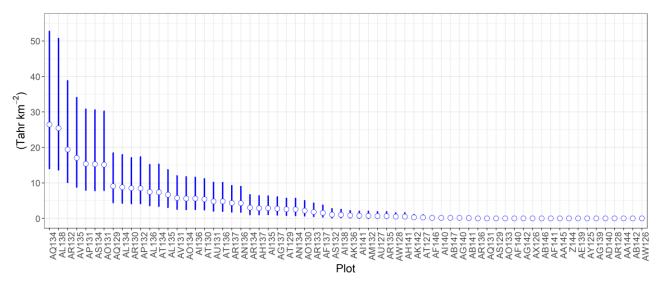


Figure 3. The estimates of average tahr density (open circles) and associated 95% credible intervals (solid lines) on each of the 66 plots sampled by aerial surveys during 2016, 2017 and 2018. The plots are shown in descending order of mean tahr density.

Table 2. Mean density of tahr (tahr/km²) within each management unit and exclusion zone estimated from 66 plots subject to aerial surveys during 2016, 2017 and 2018. SD – standard deviation; LCL – lower 95% confidence limit; UCL – upper 95% confidence limit; n – number of plots. The seven management units (MU) and two exclusion zones (EZ) are described in Table 1.

Unit/Zone	Density	SD	LCL	UCL	n
MU1	8.54	2.88	4.41	16.54	7
MU2	7.00	3.15	2.9	16.90	8
MU3	9.17	3.01	4.81	17.46	11
MU4	5.17	1.69	2.72	9.79	8
MU5	8.47	5.90	2.16	33.2	5
MU6	3.10	0.70	1.99	4.82	7
MU7	0.16	0.09	0.06	0.47	7
EZ1	0.19	0.16	0.04	0.97	4
EZ2	0.06	0.02	0.03	0.12	9

The estimated total abundance of tahr within management units and exclusion zones ranged from 100 individuals in MU7 to around 8,000 tahr in MU3 (Table 3, Figure 4). Abundance in the two exclusion zones was estimated to be around 100 – 150 individuals (Table 3, Figure 4). In general, the precision of the abundance estimates for individual management units has improved on the estimates in Ramsey (2018) with the addition of the 28 plots sampled in 2018. However, precision of estimates for some units was still low (e.g. MU5 had 95% confidence intervals of 993 – 15,274 tahr). This was a consequence of small sample sizes for some management units relative to the total number of plots available for sampling, as well as the high spatial variation in abundance estimates among plots within a unit.

The total abundance of tahr on PCL was estimated to be 34,292 (95% confidence interval; 24,777 – 47,461) (Table 4). This estimate is similar to that given in Ramsey (2018) who used data from the subset of 38 plots sampled in 2016 and 2017. Despite the low precision for estimates of abundance for some management units, the precision of the estimate of overall abundance was reasonable, having a coefficient of variation (CV) of 17% (Table 4).

Table 3. Estimates of total abundance (*N*) of tahr within each management unit and exclusion zone based on monitoring data from 66 plots subject to aerial surveys during 2016, 2017 and 2018. SD - standard deviation; LCL - lower 95% confidence limit; UCL - upper 95% confidence limit; *u* - number of sampled plots; *U* - estimated number of plots available to be sampled.

MU	N	SD	LCL	UCL	и	U
MU1	6557	2211	3386	12699	7	192
MU2	5798	2606	2402	13993	8	207
MU3	7919	2603	4157	15083	11	216
MU4	7666	2502	4043	14535	8	371
MU5	3894	2715	993	15274	5	115
MU6	2105	476	1351	3280	7	170
MU7	100	53	35	284	7	152
EZ1	150	125	29	768	4	197
EZ2	103	36	52	204	9	408

Table 4. Estimated total abundance (*N*) of tahr across the PCL during 2016, 2017 and 2018. SD – standard deviation; CV – % coefficient of variation; LCL – lower 95% confidence limit; UCL – upper 95% confidence limit.

N	SD	CV	LCL	UCL
34,292	5686	17	24,777	47,461

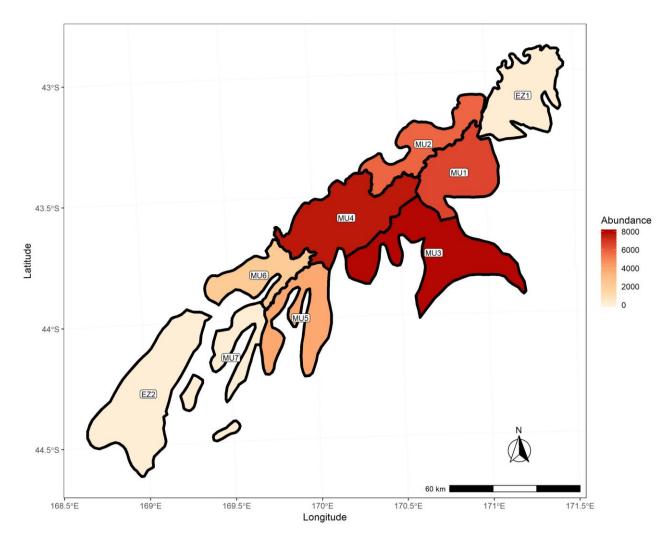


Figure 4. The total abundance of Himalayan tahr within each management unit and exclusion zone based on monitoring data from 66 plots subject to aerial surveys during 2016, 2017 and 2018.

5 Discussion

The Himalayan Thar Control Plan identified a "population of 10,000 over the entire range as a presently acceptable maximum" (Department of Conservation 1993: 2). The estimated tahr population reported here is only for the PCL, which is approximately 62% of the tahr breeding range as defined in Department of Conservation (1993). Hence, the total tahr population across the entire breeding range is likely much greater than estimated here. The tahr population on PCL (Table 4) clearly exceeds the 10,000 specified for the entire tahr range, with the lower 95% confidence limit more than double that value.

Tahr densities were highly variable across the seven tahr management units. Average tahr densities exceeded the thresholds defined in the Himalayan Tahr Control Plan (Department of Conservation 1993; Table 1) for all management units except MU7. Average tahr densities also exceeded zero in both exclusion zones. There was, however, substantial uncertainty around the estimated density of tahr for some management units. This uncertainty was most likely due to the chance sampling of high and low-density areas between years. Tahr were also potentially subject to harvesting on all plots, and any mortality occurring between the first and third counts would have increased uncertainty in the estimates of tahr abundance on plots and hence for management units.

The precision (coefficient of variation) of the tahr abundance estimates for each management unit and exclusion zone improved with the addition of the 2018 monitoring data. As there were insufficient numbers of plots sampled per year to enable annual density estimates for each management unit, our estimate of overall abundance necessarily combined plots sampled in different years. Hence, our estimates for each management unit effectively averages over any interannual changes in abundance that may have occurred. There was no evidence of any large changes over the three-year sampling period. However, due to the high variation in density among plots, we could not make any strong conclusions about the magnitude of interannual changes. Once all plots have been sampled once, and data become available for the second round of monitoring for each plot, an in-depth analysis of population trends in each management unit can be undertaken.

The variance in the estimates of abundance for each management unit and exclusion zone could potentially be further improved by stratification (e.g. habitat-based strata). Hence, more detailed maps of available tahr habitat across the PCL would be required to undertake this stratification. Further work is also being undertaken to investigate models of the relationship between tahr abundance and habitat variables. Such models could also provide an alternative means to more accurately map the distribution of tahr across each management area.

6 References

- Allen, R.B., Wright, E.F., Macleod, C.J., Bellingham, P.J., Forsyth, D.M., Mason, N.W.H., Gormley, A.M., Marberg, A.E., Mackenzie, D.I. & McKay, M. (2013) *Designing an Inventory and Monitoring Programme for the Department of Conservation's Natural Heritage Management System.* Landcare Research Contract Report LC1730, Landcare Research, Lincoln, New Zealand.
- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P. & Riddell, A. (2017) *Stan*: A Probabilistic Programming Language. *Journal of Statistical Software*, **76**, 1–32.
- Caughley, G. (1971) The season of births for Northern-Hemisphere ungulates in New Zealand. *Mammalia*, **35**, 204–219.
- Cruz, J., Thomson, C., Parkes, J.P., Gruner, I. & Forsyth, D.M. (2017) Long-term impacts of an introduced ungulate in native grasslands: Himalayan tahr (*Hemitragus jemlahicus*) in New Zealand's Southern Alps. *Biological Invasions*, **19**, 339–349.
- Dail, D. & Madsen, L. (2011) Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, **67**, 577–587.
- Department of Conservation. (1993) *Himalayan Thar Control Plan*. Canterbury Conservancy Conservation Management Series No. 3, Department of Conservation, Christchurch, New Zealand.
- Forsyth, D.M., Perry, M. & McKay, M. (2018) Field Protocols for Tier 1 Monitoring: Himalayan Tahr Abundance Monitoring Protocol Version 2.0. Department of Conservation Document DOC-2650377, Department of Conservation, Wellington.
- Humbert, J.Y., Scott Mills, L., Horne, J.S. & Dennis, B. (2009) A better way to estimate population trends. *Oikos*, **118**, 1940–1946.
- Parkes, J.P. (2009) Management of Himalayan thar (*Hemitragus jemlahicus*) in New Zealand: The influence of Graeme Caughley. *Wildlife Research*, **36**, 41–47.
- Ramsey, D.S.L. (2018) *Tahr Density Estimates from Aerial Surveys Preliminary Results*. Unpublished report to the Department of Conservation, New Zealand, https://www.doc.govt.nz/globalassets/documents/parks-and-recreation/hunting/west-coast/tahr-density-estimates.pdf.
- Skalski, J.R. (1994) Estimating wildlife populations based on incomplete area surveys. *Wildlife Society Bulletin*, **22**, 192–203.
- Thompson, S.K. (1992) Sampling. John Wiley & Sons, New York.
- Thompson, W.L., White, G.C. & Gowan, C. (1998) *Monitoring Vertebrate Populations*, 1st ed. Academic Press.

Appendix 1

Abundance model

The counts of tahr at each plot, at each time period, were used to estimate abundance corrected for imperfect detection using an N-mixture model for open populations (Dail & Madsen 2011). We treated each of the three replicate counts at each plot as potentially being open to movement (immigration/emigration) between sampling times. Hence, tahr abundance at each plot i and sampling period t (t = 1, 2, 3) was modeled as

$$y_{it} \sim Bin(p, N_{i,t})$$

where $N_{i,i}$ is the abundance of tahr in each plot i during sampling occasion t and p is the detection probability of tahr during aerial surveys. In order to estimate abundance $N_{i,t}$ at each sampling period t, it is assumed that abundance follows a first order Markov process where abundance at time t was dependent on the abundance at time t-1, using an exponential trend model as follows

$$N_{i,i} \sim Poisson(\lambda_{i,i})$$

$$\log(\lambda_{i,1}) = \eta_i$$

$$\log(\lambda_{i,t}) = \log(\lambda_{i,t-1}) + r_i T_{i,t-1}$$

$$\log(t(p)) = \phi$$

$$r_i \sim N(\mu_r, \sigma_r)$$

$$\eta_i \sim N(0, 5)$$

$$\mu_r \sim N(0, 1)$$

$$\sigma_r \sim HN(0, 1)$$

$$\phi \sim N(0, 1)$$

where r_i was the change in the (log) population size at each between period t-1 and t for plot i and $T_{i,t}$ was the time period (weeks) between sampling periods for each plot (Humbert et al. 2009; Dail & Madsen 2011). The N-mixture open population model above was fitted in a Bayesian framework using Hamiltonian Markov Chain Monte Carlo (HMCMC) sampling using Stan ver. 2.18.2 (Carpenter et al. 2017). The rate of change parameters for each plot (r_i) were modeled with a hierarchical prior distribution specified as $N(\mu_r, \sigma_r)$. Weakly informative prior distributions were placed on the initial log population abundance for each plot, $\eta \sim N(0,5)$ as well as the hyperparameters, $\mu_r \sim N(0,1)$, $\sigma_r \sim HN(0,1)$, $\phi \sim N(0,1)$. The model was updated for 6000 iterations using 3 chains with the first 1000 iterations used as a burn-in and discarded leaving 15,000 samples to form the posterior distribution of each parameter.

Appendix 2

Abundance estimates for each management unit and exclusion zone

We used finite sampling estimators assuming a stratified random sampling design (Thompson 1992; Skalski 1994; Thompson, White & Gowan 1998) to estimate total abundance within each stratum, based on incomplete surveys. Here, management units correspond to strata. If u number of plots are sampled from a total number U in stratum h, the estimate of abundance is given by

$$\widehat{N_h} = \overline{N_h} U_h$$

where $\widehat{N_h}$ is the estimate of total abundance for stratum h, $\overline{N_h}$ is the mean abundance over the u plots and U_h is total number of plots in stratum h. The estimate of variance is given by

$$\widehat{Var}(\widehat{N_h}) = U_h^2 \{ (1 - \frac{u_h}{U_h}) \frac{\widehat{S}_{N_{hi}}^2}{u_h} + \frac{\widehat{Var}(\widehat{N_{hi}|N_{hi}})}{U_h} \}$$

where

$$\widehat{S}_{N_{hi}}^2 = \frac{\sum_{k=1}^{u} (\widehat{N}_{hi} - \overline{\widehat{N}_h})^2}{u_h - 1}$$

and

$$\overline{\widehat{Var}(\widehat{N_{hi}}|N_{hi})} = \frac{\sum_{k=1}^{u_h} \widehat{Var}(\widehat{N_{hi}}|N_{hi})}{u_h}$$

The total abundance over all sampled management units is then simply

$$\sum_{h=1}^{n} \widehat{N_h}$$

with variance

$$\sum_{h=1}^{n} \widehat{Var}\left(\widehat{N_h}\right)$$

An estimate of the average density in each management unit can also be calculated as

$$\widehat{D_h} = \frac{\widehat{N_h}}{A_h}$$

Where A_h is the (2 dimensional) area of management unit h. This has variance of

$$\widehat{Var}(\widehat{D}_h) = \frac{\widehat{Var}(\widehat{N}_h)}{A_h^2}$$

Appendix 3

Figure A1. The estimates of tahr density on each of the three sampling occasions for each of the 66 sampled plots (blue open circles and lines). Black solid circles are the naïve estimates of tahr density calculated from the raw counts. For each plot, the range for the y-axis is scaled to the range of the data. The alpha-numeric (e.g., AA144) is the unique plot identifier.

