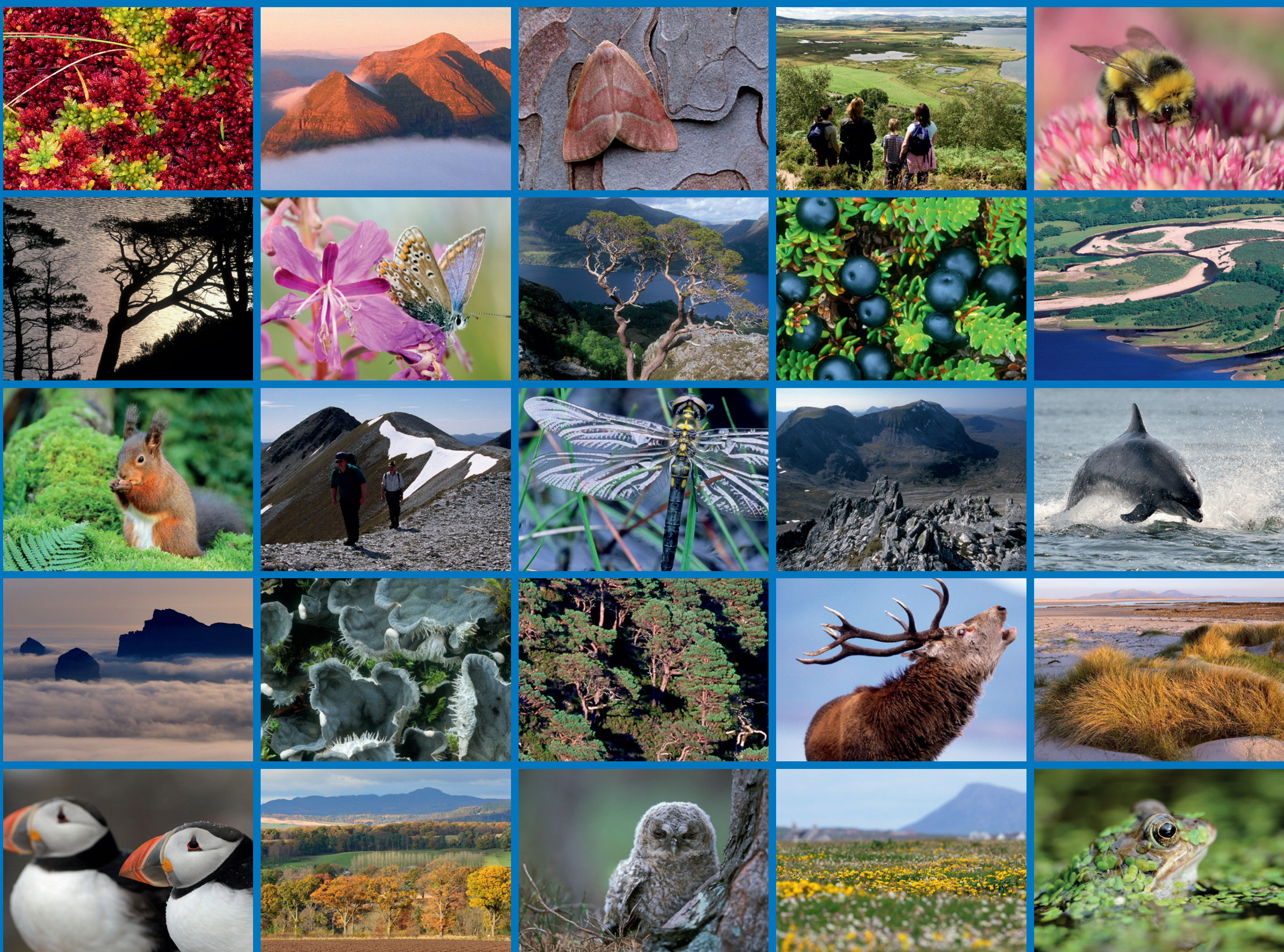
Scottish Natural Heritage
Research Report No. 1149

Updating the estimates of national trends and regional differences in red deer densities on open-hill ground in Scotland



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RESEARCH REPORT

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Updating the estimates of national trends and regional differences in red deer densities on open-hill ground in Scotland

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RESEARCH REPORT
Summary

Updating the estimates of national trends and regional differences in red deer densities on open-hill ground in Scotland

Research Report No. 1149
Project No:
Contractor: The James Hutton Institute and Biomathematics and Statistics Scotland, in collaboration with SNH
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Keywords

culling; density dependence; Highlands & Islands; natural heritage; sheep

Background

This report incorporates 30 Deer Management Area (DMA) counts of red deer on open-hill ground in the Highlands and Islands of Scotland, conducted in 2017-2019 to extend previous estimates of overall red deer density (Albon *et al.,* 2017), and describe regional variation, since systematic censuses began in 1961. The updated data set also includes 15 partial counts of DMAs conducted between 2014 and 2018, but not previously available.

No attempt has been made to translate the modelled densities into an estimate of the total size of the open-hill population, because this detracts from the variation at local scales, where impact on the natural heritage may be important. The temporal and spatial variation in population density is explored in terms of two major drivers: culling effort and density dependence. This update concentrates on changes in density over the last 20 years, during which time the previous work suggested the red deer population had stabilised after four decades of growth. This report addresses three primary questions:

- Does the updated trend in overall deer density suggest the open-hill population in Scotland remains stable?
- What local trends in deer density are revealed by the latest counts, particularly in Deer Management Areas (DMAs) where change since 2000 was not assessed in Albon *et al.,* 2017, because there was no count in the previous five years?
- Does the variation in these local trends reinforce the evidence that culling is the main driver of temporal change in deer density? Is there additional evidence that reduced competition, due to reduced hill-sheep stocks, is contributing to the variation?

Unfortunately, attempts to investigate whether the changes in red deer density were associated with the reduction in hill-sheep grazing were no longer possible because data on sheep stocks at the scale of DMUs were not available after 2015. Therefore, the third question could not be addressed, fully.

In contrast to previous the analysis for the period 1961 - 2016 (Albon *et al.,* 2017) we excluded all summer (June to September) counts because these tended to be partial counts of the DMA, and often there was uncertainty about the coverage of the very largest DMUs.

Main findings

- The national mean density of red deer on open-hill ground in the Highlands and Islands of Scotland in winter 2019 was estimated 9.35 deer km^2 (8.01 - 10.69, 95% CI). Overall there appears to have been a slight decrease (c. 9%) from a peak around 2000 of 10.25 deer km^2 (8.96 - 11.53, 95% CI). However, since estimates over the last 20 years all lie within the mean 95% confidence intervals, the current overall density does appear to be stable at about 10 deer km^2.
- Ten Deer Management Areas (DMAs) where red deer density was not estimated in 2016 had a median density of 9.6 deer km^2 (range 1.7 (Skye) - 31.4 (Glenartney) deer km^2). The updated and revised estimates across 52 DMAs confirms an order of magnitude variation from < 2 deer km^2 (Trossachs, Skye) to > 20 deer km^2 (Tayside, Glenartney).
- The latest estimates of red deer density reinforce the previous pattern of variation in density across Scotland with lower densities in the Outer Isles, Skye and most DMAs on the North-west coast, as well as the northern parts of the Grampian Mountains. Higher densities tended to occur from South Ross down the West coast to Morvern, including Mull and Jura, as well as a group of DMAs in parts of the Grampians, including Glen Isla/Glen Shee, Tayside, East Loch Ericht, and Breadalbane.
- Changes in red deer density over the last two decades varied between DMAs from decreases of >60% (Cairngorm-Speyside & Trossachs) to increases of >60% (South Uist, West Sutherland - Lochinver and East Ross). In general, densities have declined in Eastern areas; are stable in the North West, but with some increases in other areas.
- Cull rates have increased steadily since 1961, in particular the proportion of calves taken has increased markedly. Although the overall cull in 2017/18 - the last year cull-return information was available – was the highest recorded (2.6 deer km^2) the cull declined approximately 20% over the previous 20 years. In some recent years (2010 - 2012, 2015) the cull has been less than 2 deer km^2 (approximately 20% of the counted population): a cull < 22% tends to be associated with increasing population density across DMAs.
- A significant proportion (15%) of the spatial variation in population growth (changing deer density) can be attributed to differences in the level of culling which varies between DMAs from less than 10% to more than 40% of the densities estimated from the counts.
- After accounting for cull rate, spatial variation in population growth can also be attributed to differences in estimated deer density. Since high deer density is associated with low calf:hind ratios, and hence lower recruitment, the density dependence presumably reflects lower per capita resources at higher deer densities.
- Consequently, deer managers who want to have stable populations will need to cull at around 22% rather than the traditional $1/6^{th}$ (17%) of the total population and those with comparatively low-density deer populations with high calf:hind ratios will need to shoot proportionally more.
- In conclusion, we encourage SNH to i) try to establish a more consistent cull return policy in order to monitor more closely the number of animals killed, ii) to trial more regular censuses, of sub-samples of DMUs, in a systematic rolling programme across the DMAs in order to reduce the wide confidence estimates and improve the power to detect change in deer density across Scotland.

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1. THE STATUS AND TRENDS IN THE OVERALL RED DEER POPULATION IN THE HIGHLANDS & ISLANDS

1.1 Approach

Changes in the overall population density of red deer (*Cervus elaphus*) on open-hill range in the Highland and Islands, the species' stronghold in Scotland, were estimated from 'official' counts of areas coordinated by SNH, and its predecessors, the Deer Commission for Scotland and Red Deer Commission, between 1961 and 2019 (Box 1, page 2). The estimates for the three years 2017-2019, since the previous analysis (Albon *et al.,* 2017), are based on total counts of 30 Deer Management Areas (DMA). In addition, 15 SNH staff assisted partial counts conducted in the winter, between 2014 and 2018, but not previously used, were also incorporated. The full matrix of DMAs by Year count data is shown in ANNEX 1. Since for this type of analysis the counts need to be done in a consistent way, we did not use the estimates from locally-commissioned censuses undertaken by individual Deer Management Groups (DMGs), since the methods and standards are undocumented and may differ.

Even when the counts are consistently conducted, what proportion of animals present in an area of land are counted, is unknown, as is the extent to which the number of animals present at the time of the count is representative of the number of animals present over longer time periods. While some counts are thought to be under-estimates, others may involve some double-counting. Thus the 'total' count method has an unquantified error. However, it should be possible to use data from consistently-conducted counts over multiple years to estimate trends in deer densities - whether a given population is increasing, decreasing or unchanged, with more confidence, accepting that underlying, long-term trends will be at least partially hidden due to short-term fluctuations in the location of animals and other uncontrolled sources of variation in the counts.

Ideally counts would be conducted annually and, also, repeated for each spatial unit of interest, since this should permit the most precise detection of trends. As the intervals between consecutive counts increase, estimation of what has happened in the intervening period is likely to become less precise.

Within each DMA, Deer Management Units (DMU – the properties/estates) named as Forestry Commission (now Forestry and Land Scotland) land were excluded, because of the difficulty of estimating numbers in largely wooded areas. It was not possible to exclude privately owned forestry in a systematic way. However, wooded land is not generally counted, either on foot or from helicopters.

BOX 1: The 'official' count data

The data used were all the 'foot' counts conducted since 1961, by the Red Deer Commission for Scotland and its successor the Deer Commission for Scotland, as well as subsequent counts by SNH. The maps used to record deer by the counters were digitised by the Macaulay Land Use Research Institute. After 2001, the counts were done from a helicopter‡ or, in some cases, a combination of 'foot' counts and helicopter counts. Counts undertaken by local Deer Management Groups (DMGs) including some digitised by SNH have been excluded from the analysis to ensure consistency in methods.

In contrast to the last assessment (Albon *et al.,* 2017) all Summer counts (Jun – Sep) were excluded, because generally these were partial counts, covering only a proportion of the Deer Management Units' (DMUs) land-holdings, and in some cases an unknown proportion of the largest DMUs, within the Deer Management Area (DMA). Also, this time we analysed the data across 'Deer-Years', so that Autumn (Oct – Dec) counts in calendar year t were regarded as part of the period including Winter (Jan – May) in calendar year t_{+1}. Occasionally, there were two or more counts of the same DMA within the same Deer-Year. If there was both an Autumn count and a Winter count in the same Deer-Year the Winter count was selected because these were more numerous overall, and often covered a higher proportion of the DMUs. Where there were two counts in the same Winter the one covering the larger number of DMUs was selected. Counts were downloaded from http://gateway.snh.gov.uk/natural-spaces/index.jsp as digitised points within polygon shape files, with one or more polygons for each DMU.

The number of DMAs has increased over time either because new ones were formed (e.g.: South Uist, first counted in 2000) or some of the larger ones have been subdivided, recently (e.g.: East Grampian, South Ross, West Sutherland, split into 4, 5 and 4, respectively). We have used these sub-divisions over the entire period. Two DMAs, South Sutherland and West Loch Lomond, were counted only once, and excluded from the analysis because there was no information on the trends.

Our analysis is based on 632 'official' counts of 53 DMAs (counted three or more times) over 59 Deer-Years, with 30 DMAs counted after 2016, and all bar two of the 53 DMAs in the last five years. ANNEX 1 shows the distribution of 'full' (> 50% DMUs counted) and partial counts (< 50% DMUs counted) across DMAs since 1961 used.

Within each DMA we excluded all DMUs labelled as 'Forestry and Land Scotland' holdings because of the difficulty of estimating deer in 'parcels' of land which are predominantly wooded. Typically, DMUs are individual estates/properties, though some of the largest estates are made up of two or more DMUs. There were 532 'parcels' of land which had no deer recorded in any count. Typically, these were small (median 55 ha) and were excluded. The analysis used 852 DMUs which recorded at least one deer in one count. Where no deer were recorded on a specific count of a DMU it was retained in the analysis when more than 50% of the land area had been covered in the census. This threshold was imposed to avoid false zeros arising from only partial coverage of DMUs. The previous analysis (Albon *et al* 2017) failed to recognise the problem of 'true' zeros, and inadvertently excluded all zero densities. All counts were calculated as densities of all deer (stags, hinds and calves) per unit land area, excluding large bodies of water but not woodland. All densities are expressed as the number of deer km^2.

‡*Two independent studies of the reliability of estimates from 'foot' counts versus helicopter counts suggest that there is no systematic difference in the estimates of numbers from the two methods. A study on Letterewe Estate found variable results, with helicopter counts giving higher estimates than foot counts only on very rugged, high ground (Milner et al 2002). While the Deer Commission for Scotland demonstrated that in two of three test sites, ground counts were 10% higher than helicopter counts (Daniels 2006). In the third site, Rum, the helicopter counts averaged just 4% higher. In each of the three test sites the variability between the repeat counts (coefficient of variation) was similar for both methods. However, the latter study showed that when groups of more than 100 deer are observed from a helicopter, a digital image gives a higher number than the immediate visual estimate.*

BOX 2: Statistical Methods

Approach: The deer densities, calculated from the counts for each DMU, show considerable fluctuation over time. Some statistical analysis of these densities is required to separate underlying trends which are of interest from unrealistic, short-term, fluctuations which we have considered to be random noise. The trends will be most robustly estimated where we have many counts. The presence of both long-term trends and short-term fluctuations can be seen in the data from Rum, a DMA which, being an island some distance from the mainland, has a self-contained population. For Rum, we know some counts must be under-estimates, and/or others may involve an element of double-counting, because the observed increases in counts between consecutive years is not possible given the level of the cull. A similar effect is likely to occur in other DMUs and DMAs where any one count may be an under-estimate or over-estimate and as a result may not fit very well with the long-term trend.

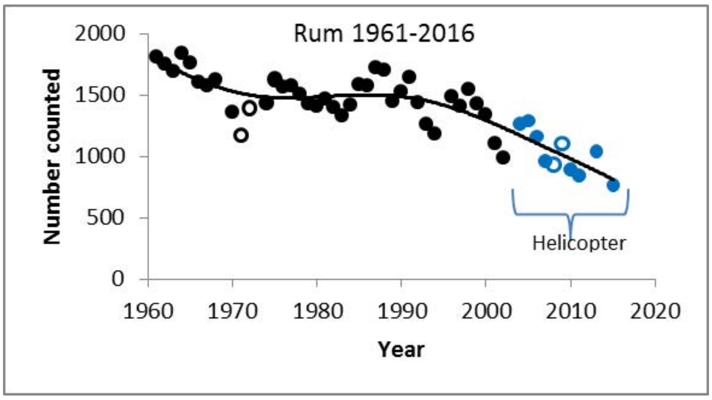

Figure B2. The trend in red deer counts on Rum since 1961. Open circles show consecutive counts (1971 & 1972, and 2008 & 2009) where the apparent increases (>18%) were unlikely given the size of the cull. Individual counts can be anomalous but statistical analysis smooths these out to produce the estimated trend line.

Fitting models to estimate the trend: We have estimated long-term trends in red deer densities at both the national level and at the DMA level from the DMU-level data, making allowance for differences between the DMUs and, in the case of national trends, for differences between DMAs. Densities take into account differences in DMU area, which are used as weights, so that trends are representative of changes in the overall population size. As counts were not available for every DMU in every year, we use a statistical model to estimate densities. These modelled values provide predictions in cases where there is no count as well as fitted values in cases where there is a count.

'Good' practice in analysing density data such as these is to convert the values to the log scale so that they have a less skewed (i.e. a more 'normal') frequency distribution and the possibility of negative predictions from the model is avoided. However, a disadvantage is that there is a bias when predictions from the model are back-transformed to the untransformed scale. A second disadvantage is that whereas the area-weighted average of the untransformed densities from the individual DMUs that form a DMA is equal to the density calculated over the DMA as a whole, this no longer applies if a weighted average of log-transformed data is used. As this analysis is primarily concerned with prediction rather than hypothesis testing, the assumption of normality is less important, and we have therefore chosen to carry out the analysis on the untransformed scale. Thus, the approach adopted here differs from the previous analysis (Albon *et al.,* 2017) which modelled the log transformed data.

Technical details: The procedure for fitting the models was to fit a Generalized Additive Model (GAM), with a smoothing spline for year, to the estimates of annual densities either from all Deer Management Units (DMUs) or from DMUs within a particular Deer Management Area (DMA) using the Mixed GAM computation vehicle, 'mgcv', statistical package (Wood, 2006) in R (R Core Team, 2016). In most cases the smoothing parameter was selected automatically, but in a few cases where visual inspection suggested that the fitted spline provided a poor fit to the data, and so the 'sp' parameter was adjusted manually. In addition to the smooth trend term, the models for particular DMAs each contained a categorical fixed effect to account for differences between DMUs, whilst the national level analysis contained categorical random effects to account for differences between DMUs and for differences between DMAs. The DMU land areas were used as weights.

Deer counts were downloaded from the SNH http://gateway.snh.gov.uk/natural-spaces/index.jsp as digitised points within polygon shape files, with one or more polygons for each DMU. The median number of counts for any individual DMA was 11, and the most 42 (Rum), while the number of DMAs counted per year varied from four to 23, with the median 11 (ANNEX 1).

Deer densities were calculated as the number of red deer per km^2, after excluding water. Possible changes in land use were not quantified. The data used in the statistical analysis were at the level of DMUs, although predictions were obtained at the regional level of Deer Management Areas (DMAs) and at the national level (see Box 2, page 3/4). These are equivalent to DMGs but we use this term to allow us to include areas where some DMGs have lapsed e.g.: Cabrach & Glenbuchat, or to include all parts of the area counted when some of this area might be outside a DMG boundary (e.g.: Islay). DMAs are similar to the Deer Count Areas once used by the Deer Commission for Scotland.

In this section, we analyse national trends in both total deer densities and changes in recruitment (the number of calves per 100 hinds counted).

1.2 Results

Having refined the analysis as far as possible within the limitations of the data, the results show that the overall mean density of red deer on open-hill range in the Highlands and Islands increased steadily from 1961 until around 2000, since when densities have remained more-or-less stable (Figure 1, page 5). The fitted model suggests that over the last two decades there has been a slight decline (c. 9%) from a maximum of 10.25 deer km^2 (95% CI: 8.96 - 11.53) in 2000, to 9.35 deer km^2 (95% CI: 8.9 - 10.69) in 2019. However, this recent decline should be treated cautiously given the comparatively wide confidence interval of the fitted trend (the grey shading around the black line in Figure 1). Ideally one would have greater power to detect change, but this would require a more systematic rolling programme census design. We return to this issue later in the Report.

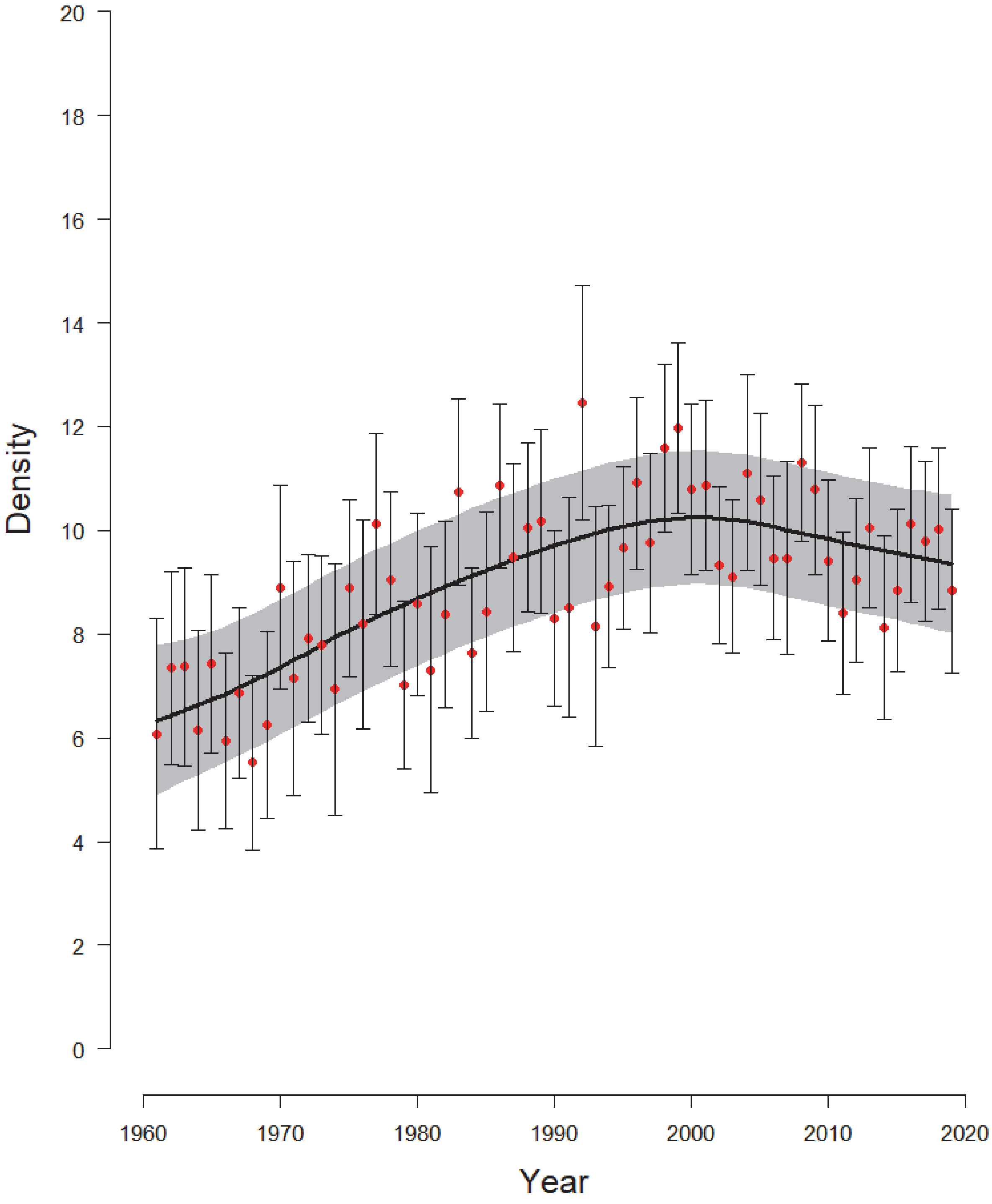

Figure 1: The overall trend (black curve – grey shading shows the 95% confidence intervals) in red deer (stags, hinds, calves) density estimated across the Highlands and Islands, since records began in 1961 until 2019. The red dots show the annual estimates and the thin lines the 95% confidence intervals based on the subset of DMAs counted in each year.

Recruitment (the number of calves counted per 100 hinds counted) varies significantly between years and overall has declined from around 40 calves per 100 hinds in 1961 to around 34 calves per 100 hinds in 2019 (Figure 2: slope = -0.098 ±0.029, $P < 0.001$). Since deer densities have risen over the last 60 years, we added hind density to the model, too. While hind density accounted for significant variation in recruitment in both time and space (slope = -0.514 ±0.036, $P < 0.001$), the decline in recruitment over time was slightly lower but still significant (slope -0.087 ± 0.036, $P < 0.004$).

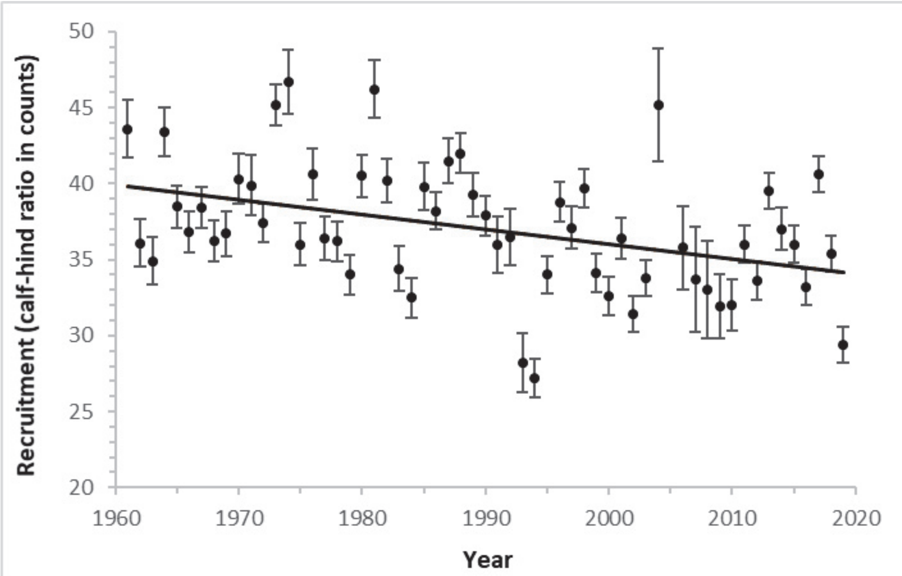

Figure 2: Annual estimates (mean ± SE) of recruitment (the number of calves counted per 100 hinds) from 1961 – 2019. The regression line shows a significant decline.

1.3 Discussion

1.3.1 Overall deer density

After four decades of steady increase since systematic surveys began in 1961, mean red deer density in the core range appears to have stopped rising around 2000. Over the last two decades the mean density has fluctuated around 10.0 deer km^2. This estimate is slightly lower (c. 0.5 deer km^2 or 5%) than in the previous analysis using data up to, and, including 2016 (Albon *et al* 2017). While well within the confidence interval of the current estimates there are at least two reasons which may have influenced the latest estimate. First, we have excluded the summer counts (Jun – Sep), because generally these were partial counts, covering only a proportion of the Deer Management Units' (DMUs) land-holdings, and in some cases an unknown proportion of the largest DMUs, within the Deer Management Area (DMA). Also, these counts were after calving and before the hind culling season, so the population characteristics were different to the winter counts, which make up more than 85% of the data base. Some of these summer counts generated very high densities. Second, in recompiling the data for this analysis it became clear that the records of no deer had been inadvertently excluded in the previous analysis (Albon *et al.,* 2017). This arose because the GIS extraction selects points (groups of deer) and 'none' in a DMU polygon was erroneously entered as missing. This time we recorded zeros where there was clear evidence that more than 50% of the DMU had been surveyed. If less than 50% was counted, we excluded the DMU. Although the 'zero' counts tend to occur on smaller DMUs, and the density estimates are area-weighted, it will nonetheless tend to 'pull' the mean slightly lower.

Since the latest analysis included 30 DMAs re-counted in the last three years, as well as 15 SNH staff-assisted partial counts conducted between 2014 and 2018 but not previously available, there were only two (Archocy/Port Clair, Northern) of the 53 DMAs which have not been counted in the last five years. Thus, these most recent estimates are both more up-to-date and robust than the previous analysis, when 20% of the DMAs had no estimate of deer density in the five years between 2012 and 2016.

1.3.2 Recruitment

Since 1961 recruitment (the calf-hind ratio in the counts) has declined significantly. Although calf-hind ratios are very variable between consecutive years, probably due to the harshness of winter weather (Clutton-Brock & Albon, 1989), the decline is not simply due to the increasing density, since the decline persists after allowing for both temporal and spatial variation in hind density.

The apparent levelling-off in the population growth was first noted by Clutton-Brock and colleagues when analysing the Deer Commission for Scotland count data up to 2000 (Clutton-Brock, Coulson & Milner, 2004). These researchers attributed a slowing in population growth in the 1990s to ‘density dependence’ in response to grazing competition for forage. Reduced recruitment as illustrated here (Figure 2) is an expectation of density-dependence. However, given that there has been a 40% reduction in sheep stocks across the Highlands & Islands since the early 1990’s (SAC, 2008; Thomson, 2011), many of which in summer, at least, competed for the hill grazing, one would not have expected to see strong density dependence, because there should be more forage *per capita*. At the same time climate warming has seen earlier springs, longer growing seasons, and hence higher plant productivity, as well as more benign winters, all of which should enhance birth rates and survival (Albon & Clutton-Brock, 1988; Clutton-Brock & Albon, 1989).

We discuss the possible reasons for this cessation of population growth and decline in recruitment later in the report (see Section 3.). Meanwhile in the next section (Section 2) we explore the differences in trends between DMAs across Scotland.

2. WHAT LOCAL TRENDS IN DEER DENSITY ARE REVEALED BY THE LATEST COUNTS, PARTICULARLY WHERE CHANGE SINCE 2000 WAS NOT ASSESSED, PREVIOUSLY

2.1 Approach

Wherever a DMA had three or more 'official' counts (Box 1, page 3) we used the smoothing spline (Generalised Additive Model – GAM: see Box 2) to predict the trend over time for each DMA (Figure 3, Annex 1) and from this a density estimate can be extracted for any one year. This permits the comparison of densities across space at the same time, as if the DMAs were all counted in the same year(s). For example, in 2000 (Figure 4: left-hand panel) or using relatively recent data to predict the status in 2019 (Figure 4: right-hand panel), we can estimate the regional variation in deer density.

For completeness we end this section with a description of the average spatial variation in calf;hind ratios from the counts, as an index of recruitment (Section 2.4), which as we have seen earlier is density dependent.

2.2 Recent temporal trends in density in DMAs not estimated in the previous review

The ten DMAs where trends were not estimated in the previous review (Albon *et al.,* 2017), represented the full range of densities across Scotland in 2000, from the lowest (South Uist : 1.37 deer km^2) to the highest (Glenartney: 29.1 deer km^2). In four of these DMAs (Skye, Strathtay, West Lochaber and Glenartney) there was little change (all between 10% decrease and 10% increase) in estimated density between 2000 and 2019 (Table 1). However, in the other six DMAs (East Loch Shiel, East Sutherland, the Gariloch Conservation Unit, Cabrach/Glenbuchat, Inverary/Tyndrum & South Uist) all deer densities increased by more than 20%, with the low-density population on South Uist increasing by 65% from an estimated 1.37 deer km^2 in 2000 to 2.26 deer km^2 in 2019 (Table 1). Median density across these ten DMAs in 2019 was 9.88 deer km^2, close to the national mean density of 9.35.

2.3 Temporal trends across all DMAs

The trends in deer densities in all DMAs since the first counts (most beginning in the 1960's) are shown grouped together regionally in Figure 3. As would be expected from the overall national density, many DMAs have increased since counts began. However active management interventions to reduce numbers locally can be clearly seen, including in Breadlabane, Cairngorm/Speyside, East Grampian – in general, Monadhliath, North West Sutherland, Rum, the Trossachs, and Wester Ross. Between 2000 and 2019 deer densities in all these DMAs have been reduced by 35% or more. This is illustrated in more detail later (ANNEX 2).

Table 1. The ten DMAs where deer density trends after 2000 were not estimated in the previous review, ordered by percentage change between 2000 and 2019.

Deer Management Area	Density 2000	Density 2019	% change
Skye	1.84	1.69	-8.0
Strathtay	17.49	17.15	-2.0
West Lochaber	13.36	14.33	+7.2
Glenartney	29.10	31.39	+7.9
East Loch Shiel	8.48	10.26	+21.1
East Sutherland	11.35	14.29	+25.9
Gairloch Conservation Unit	2.61	3.33	+27.9
Cabrach/Glenbuchat	6.87	9.49	+38.2
Inverary/Tyndrum	6.23	8.63	+38.5
South Uist	1.37	2.26	+65.0

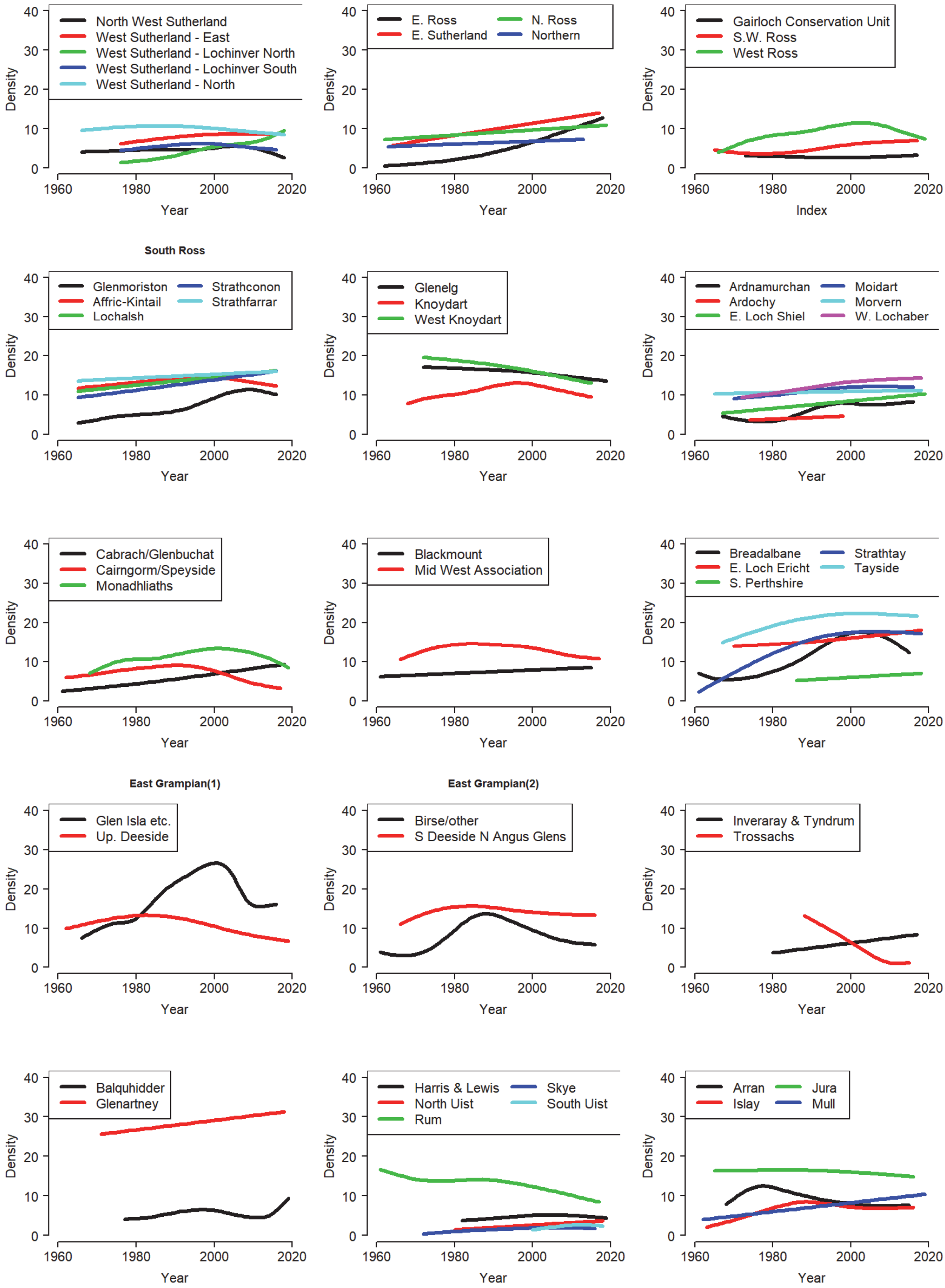

Figure 3: The temporal trends (smoothing splines) in red deer (stags, hinds, calves) density (deer per km^2) between the first and last counts of each DMA. Adjacent DMAs are grouped from the north-west mainland (top-left panel) moving south and east ending with the Islands (bottom-right). The actual densities in the years the counts were conducted are shown for each DMA in ANNEX 2.

2.4 Spatial variation in red deer density between DMAs

At the peak around 2000 red deer (stags, hinds and calves) density estimates across Scotland differed markedly (Figure 4, left-hand panel). There was a 15 to 20-fold difference from South Uist and Skye (1.4 & 1.8 deer km^2, respectively), to East Grampian – Glen Isla/Glen Shee and Glenartney (26.6 & 29.1 deer km^2, respectively). Densities were typically lower in the Outer Hebrides, (Harris/Lewis, North & South Uist) and Skye, and the North-West Highlands. The higher densities tended to occur in much of Ross-shire, West Inverness-shire, and much of Eastern Scotland. At this time ten (19%) DMAs, amounting to approximately 14% of the deer range within the Highlands & Islands of Scotland, had estimated densities >15 deer km^2. Although by 2019 there was still a 20-fold difference in density between DMAs (lowest: Trossachs, 1.65 deer km^2; highest: Glenartney, 31.4 deer km^2,), what is striking in comparing the 2019 distribution of densities with the situation in 2000 is the proportion of DMAs that are around the average density (8 -11 deer km^2). This is due to some large DMAs in the western part of the Grampian Mountains declining (Monadhliaths, Mid-West Association & Breadalbane), while others adjacent and contiguous to this have increased (Blackmount, Inverary/Tyndrum & Balquidder) (Figure 4).

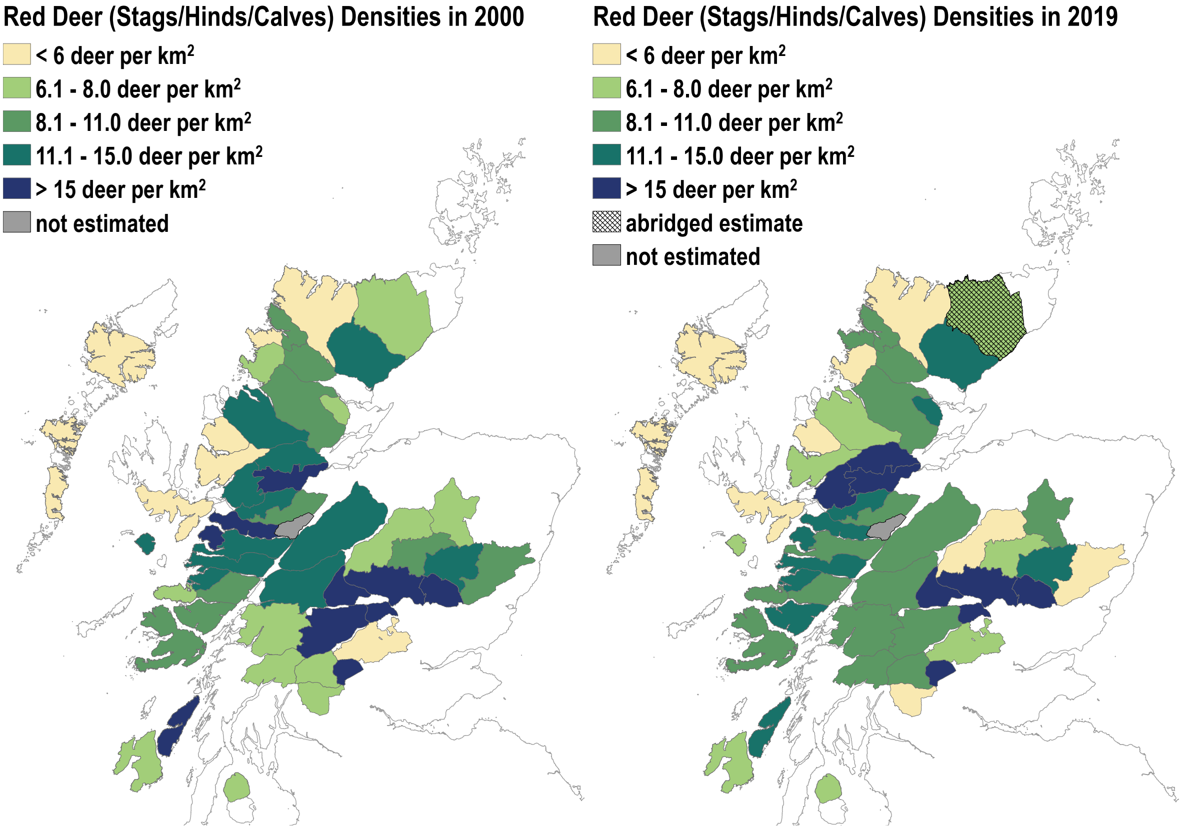

Figure 4: The spatial variation in red deer (stags, hinds, calves) density between DMAs in 2000 (left-hand panel) and in 2019 (right-hand panel) estimated from the temporal trends (smoothing splines – see Figure 3), where at least one count in last five years. Ardochy/Port Clair – last counted 1998 (grey shading) and Northern last counted in 2013 is hatched, where the extrapolation of density to 2019 needs to be treat with caution.

2.5 Differences between DMAs in the pattern of change in density since 2000

Although, we used all the winter (Oct -May) data since counts formally began in 1961 to estimate trends (see Figure 3 above: Annex 2 shows the detailed fit to the density data for each DMG), the remaining analysis concentrates on describing the changes over the last two decades, the period when the mean red deer density in the Highlands & Islands has remained more or less unchanged (Figure 1). At a regional scale, detecting geographical patterns can be difficult because often adjacent DMAs have markedly different trends (Figure 5). For example, North West Sutherland and East Sutherland have decreased >35% and increased >25%, respectively (Figure 5, right-hand panel). Nonetheless, deer densities in several large and contiguous DMAs in the northern and central Grampian Mountains have decreased markedly (>35%), including the Monadhliath, Cairngorm/Speyside, East Grampian- Upper Deeside. Glen Isla/Glenshee, Birse. While west of the Great Glen there are smaller pockets of declining density (10 - 35%), including Knoydart, West Knoydart, Glenelg, South Ross – Kintail/Affric.

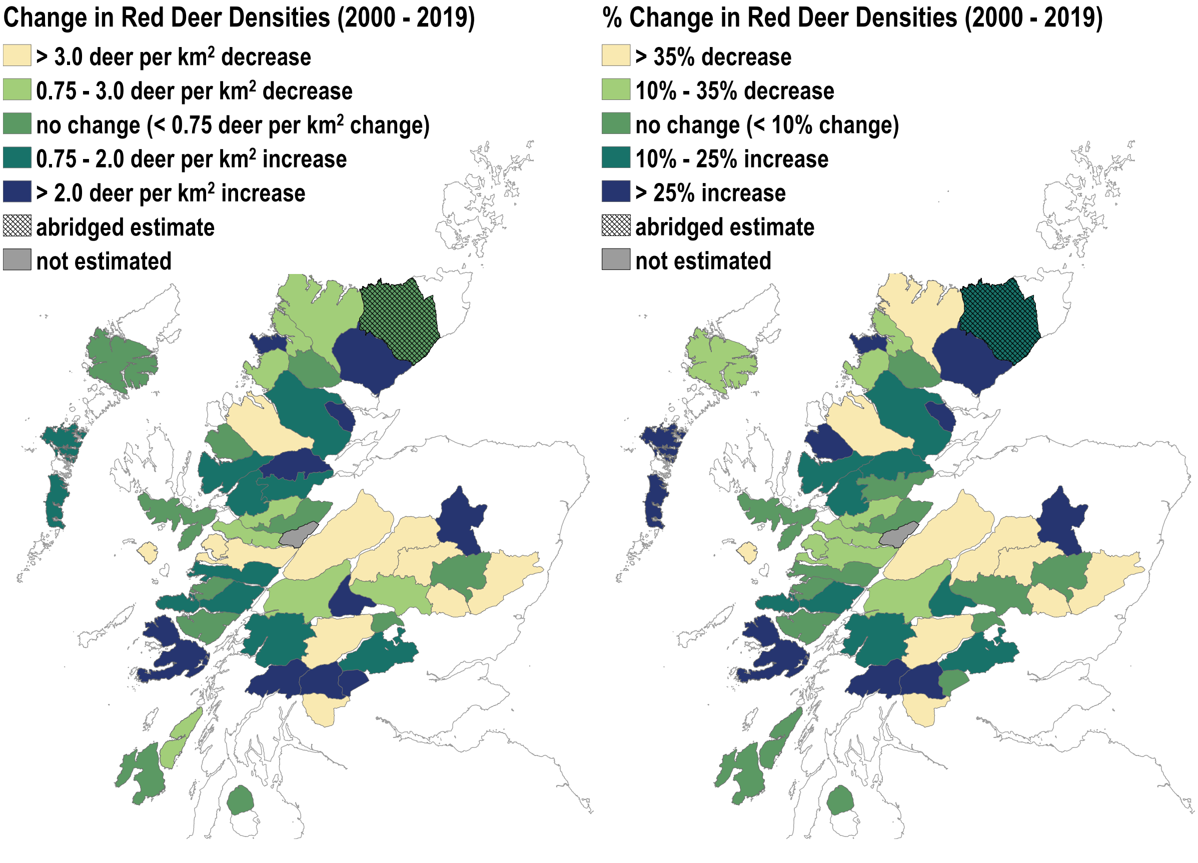

Figure 5: Differences in the magnitude of change in red deer density (stags, hinds, calves) between 2000 and 2019 derived from the trends (smoothing splines – see Figure 3), Left-hand panel - absolute change in density, right-hand panel - the % change in density. The grey shading is for Ardochy/Port Clair not counted since 1998, and the hatched area Northern DMA last counted in 2013, where the extrapolation of density to 2019 needs to be treat with caution.

2.6 Differences between DMAs in the potential recruitment to the local population

The number of calves counted per 100 hinds varied significantly across Scotland, with the DMAs on the islands, some of the west coast, Cairngorms/Speyside, the Trossachs, and South Perthshire having the highest potential recruitment (Figure 6, left-hand panel). While most of Ross-shire, the Central and Easter Grampian Mountains have lower potential recruitment. This pattern of calf:hind ratios suggests an association with typically lower densities (Figure 6, right-hand panel) on the islands and west coast, and higher densities in the central and eastern regions.

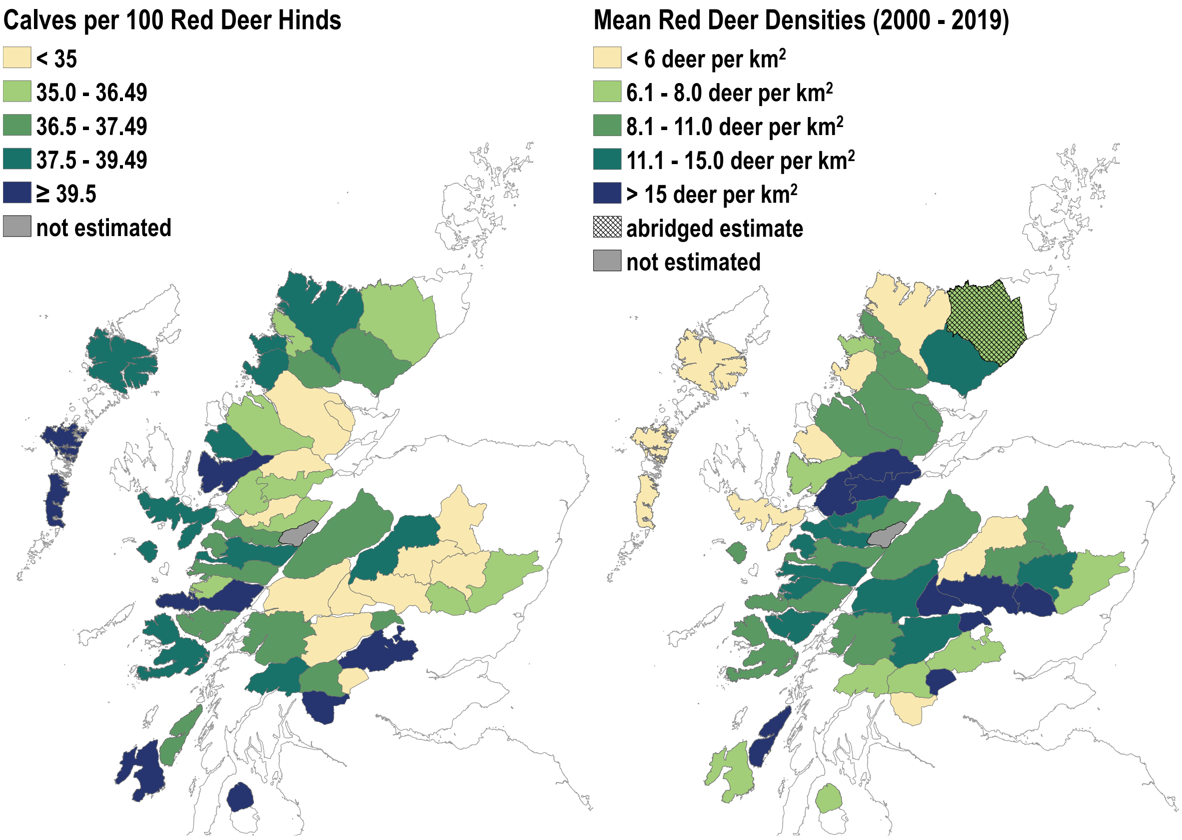

Figure 6. Spatial variation in the number of calves counted per 100 hinds (left-hand panel), a measure of potential recruitment, and (right-hnad panel) the mean deer density (2000-2019)

When the average calf:hind ratio (adjusted for the variation between years) for DMAs was regressed on the mean density estimates from 2000 and 2019 for those same DMAs, there was a significant negative relationship (Figure 7). Density (on the log-scale) accounted for 42% of the variance in the potential recruitment. Density-dependent birth and death rates, and by implication recruitment rates, have been documented previously both within populations (Clutton-Brock *et al.*, 1982; Clutton-Brock & Albon, 1989) and between some populations (Albon *et al.*, 1983). However, this is the first occasion that density-dependent potential recruitment has been demonstrated at the scale of variation across the Highlands and Islands.

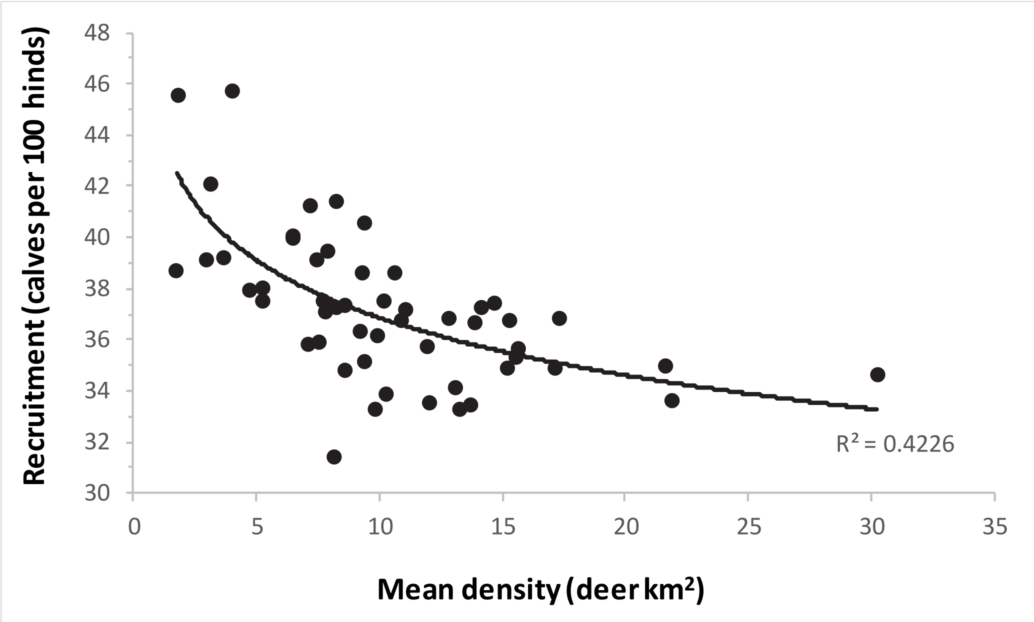

Figure 7. Spatial variation (between the DMAs) the number of calves counted per 100 hinds, a measure of potential recruitment. The fitted log-linear regression line shows the significant decline with increasing density.

3. THE DRIVERS OF OVERALL AND REGIONAL TRENDS IN DEER DENSITY

3.1 Approach

Here we explore the relationships between both spatial variation in red deer density, and temporal changes over the last two decades, in terms of two potential drivers of spatial differences. First the level of culling (see Box 3), and second, changes in sheep stocks, which, in summer at least, may compete with red deer for hill-grazing. Both of these drivers were found to have negative impacts on deer density across the Highlands and Islands between 1961 and 1985 (Clutton-Brock & Albon, 1989). However, 30 years on Albon *et al* 2017 found no evidence of an effect of sheep densities at the DMA scale, but did find a negative effect at the smaller, parish scale. Nonetheless, given the effort to update the counts of DMAs where estimated densities were not made in 2016, the possibility of an association with variation in sheep stocks is assessed again. In addition, because of the inherent density dependence in herbivore-plant systems we have taken account of the starting estimated population densities in 2000 when looking at the population change in DMAs over the last two decades.

3.2 Variation in culling levels

3.2.1 Overall trends in culling

The number of red deer hinds, stags and calves culled per km^2 has increased markedly since 1961. In the 1960s and 1970s similar numbers of stags and hinds were shot, but very few calves were shot because yeld hinds (those without a calf) tended to be selected (Figure 8).

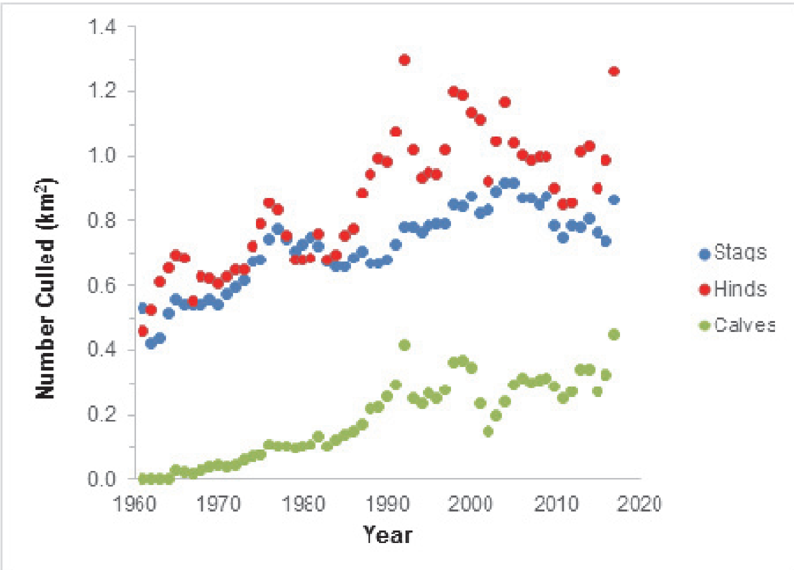

Figure 8: Trends in mean number of stags, hinds and calves culled per km^2 from 1961/62 - 2017/18. Between the years the standard errors varied for stags (0.063-0.076), for hinds (0.079 –0.10) and for calves (0.022-0.033)

BOX 3: Cull data

Approach: Not all Deer Management Units (DMUs – estates/properties) make cull returns every year, and some historical data appears to have been lost in transfer between computer software systems within and between the different statutory institutions. Albon *et al.,* 2017 noted there was a reasonable coverage of most Deer Management Areas (DMAs), though this also varied between years within DMAs. For example, between 2005/6 and 2014/15 a mean of 82.5% of DMUs reported culls, equivalent to 91% of the deer range area (excluding water). The disparity suggests smaller estates/properties are less likely to make cull returns. While many of these non-returns may be from DMUs that are not deer stalking estates, and cull very few or no deer, among those DMUs that do make regular returns there was strong statistical evidence of a negative relationship between the numbers culled per km^2 and the land area ($P < 0.01$). This under reporting means that calculations based on apparent absolute numbers culled need to be treated as minimal estimates. Consequently, the analysis of cull data used the numbers culled per km^2, weighted by the area of each DMU.

When collating the cull returns this time, we noticed that the number of non-returns has increased significantly since 2005/6 by as many as 12 DMUs per annum (Figure B3). At some stage the reduction in the available cull data may compromise the interpretation of the drivers of deer trends.

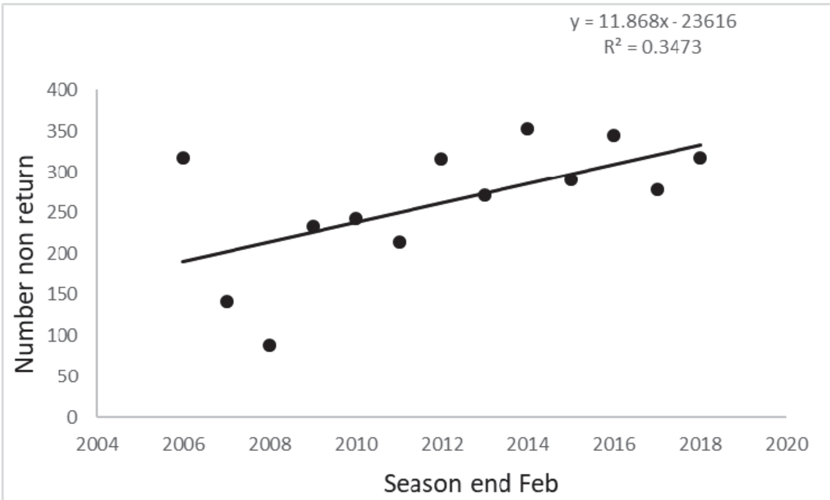

Figure B3. The number of cull non-returns plotted against the season (Jul-Feb) since 2005/6 until 2017/18.

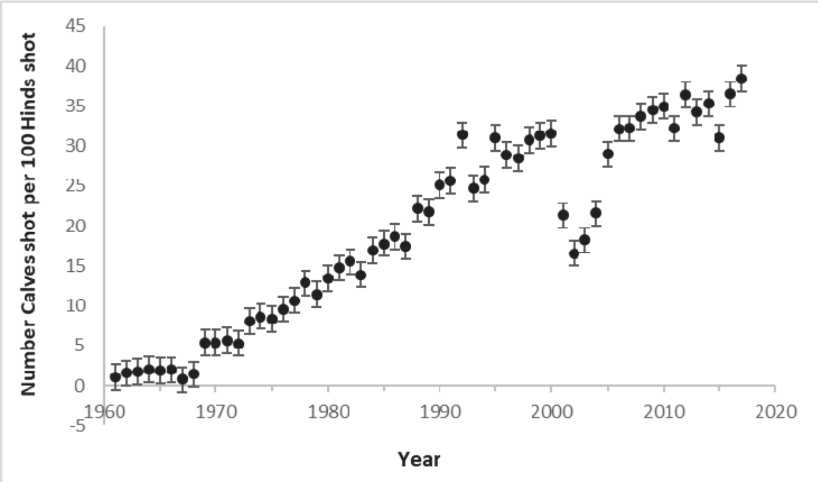

Figure 9: Trends in number of calves culled per 100 hinds (with ±SE) 1961/62 - 2017/18.

From the mid-1980s onwards more hinds than stags were shot, and increasingly milk hinds and their calves were selected: for every 100 hinds culled the number of calves culled now regularly exceeds 35, increasing year on year over the first 40 years (Figure 9). Although there was an unexplained drop between 2001-2004 (mean = 19.6), the trend for relatively more calves to be culled has continued from 2005 to present at about 4 calves per decade (slope b = 0.436 ± 0.148, t =2.94, P = 0.013).

By 2000 the total number of red deer culled averaged around 2.2 km^2. Although there was a record cull in the 2017-18 season (2.6 deer km^2 Figure 10), the total number culled per km^2 fell significantly over the previous 20 years (Figure 10). In addition, there appears to be an increasing number of non-returns (Box 3), which is worrying for although it does not influence our annual estimates of cull per unit area, we are calculating the cull across diminishing areas year on year.

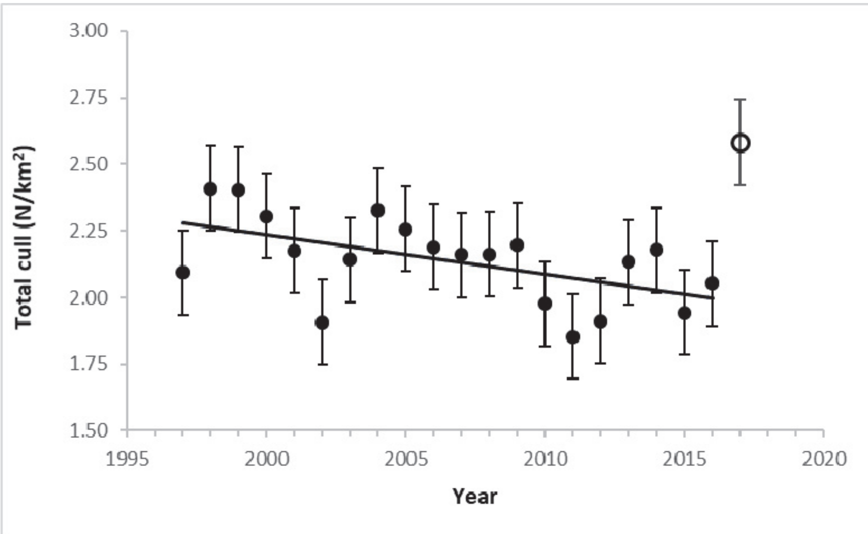

Figure 10. The total number of deer (stags, hinds & calves) culled per km^2 plotted each year since 1997/8. The fitted regression line ignores the 2017/18 season (open circle) but shows a 20% decline over the previous 20 years.

Given the mean density estimate of 10 deer km^2 and the recent level of culling about 2.2 deer km^2 (approximately 22% of the stock), and average recruitment over the last 20 years is around 35 calves per 100 hinds, the apparent total cull rate of 22-23% is higher than the recruitment (17.5%, assuming equal sex ratio of calves in the count), and likely to drive the average population downward. Early studies on Rum (Lowe, 1969) suggested that a cull of 1/6th (17%) was sufficient to limit population growth. This was based on a calf-hind ratio of around 33 (both sexes) per 100 hinds, but in practice because of misclassification of sex/age the actual cull rate turned out to be 19% of hinds in the reconstructed population. At this cull rate the Rum population declined, although this decline was attributed to the cessation of muirburn after the removal of sheep, rather than culling, *per se* (Lowe, 1969).

3.2.2 Regional variation in culling and impact on trends in deer densities across Scotland

The percentage of the estimated population culled varied markedly across the DMAs (Figure 11; left-hand panel) from as little as 13% in Glenelg and South Ross-Lochalsh, to more than 50% in East Grampian - Birse, Skye and Trossachs. The median percentage cull across the DMAs was 23%, as would be expected given a mean total cull 2.25 deer km^2 and mean density of c.10 deer km^2 (see above).

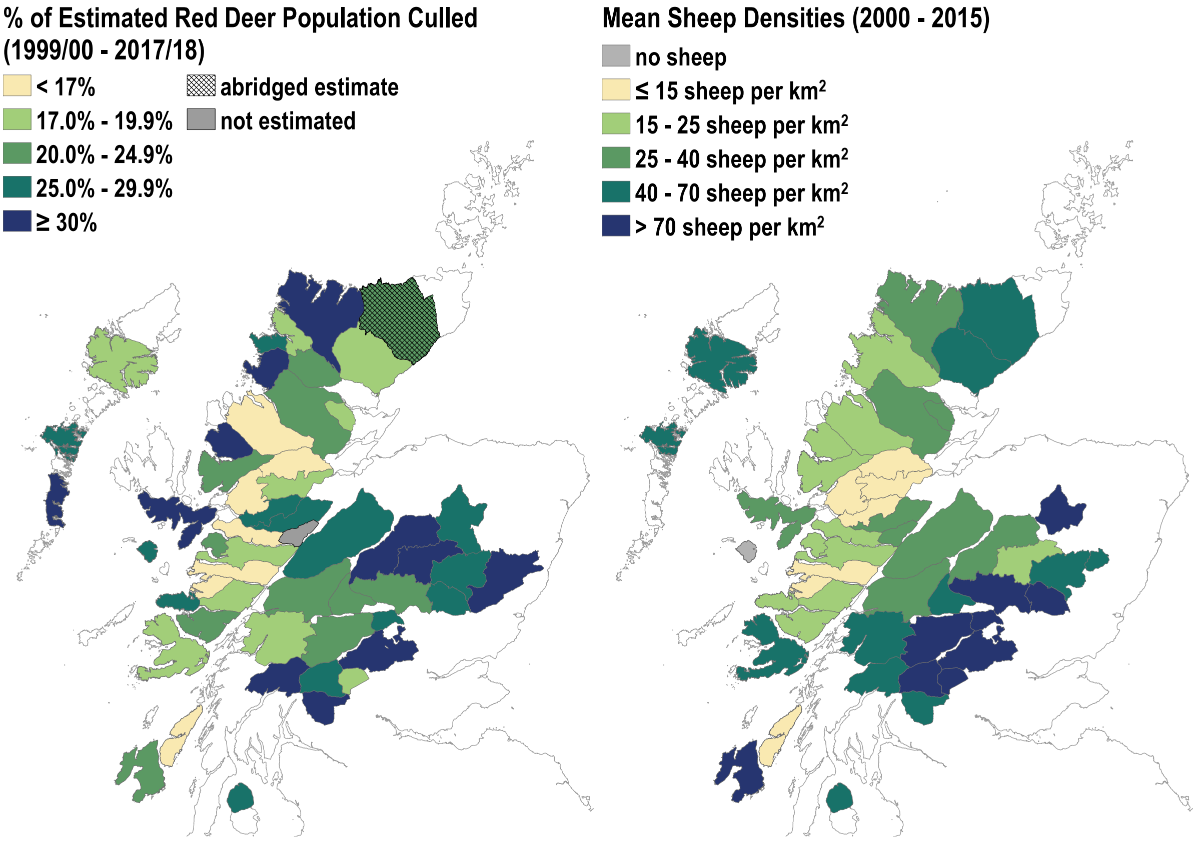

Figure 11: Variation in the mean percentage of the estimated population culled between 1998/99 and 2017/18 (left hand panel) and mean sheep densities between 2000 and 2015 (right-hand panel) across the DMAs in the Highlands and Islands.

Table 2: The estimates of the slopes, standard errors and 95% confidence intervals of the mean percentage cull and estimated density in 2000 in the model of population growth (Lambda: Log (density 2019) – Log (density 2000)) in DMAs between 2000 and 2019, with t-tests and associated statistical significance levels.

Parameter	**estimate**	**s.e.**	$t_{(50)}$	**t pr**	**lower 95%CI**	**upper 95%CI**
Constant	0.867	0.188				
% cull	-0.0225	0.0047	-4.80	<0.001	-0.0320	-0.0131
Density 2000	-0.0320	0.0086	-3.71	<0.001	-0.0493	-0.0146

To explore the extent to which these varying levels of culling could be driving the changing densities in DMAs over the last two decades we regressed the population growth rate (lambda) between 2000 and 2019 on the percentage cull. Culling alone explained 14.9% of the variation in population growth rate (slope = -0.0149 ± 0.0047SE, t = 3.15, df=50, P < 0.01). In general, when the culling level was less than 22% the population increased, but when greater than 22% it declined. Since recruitment (calves per 100 hinds) is density dependent, we also added density in 2000 to the model (Table 1, Figure 12). Both terms contributed significantly to the model between them explaining 32.1% of the variation in population growth rate. The estimated slope of the percentage cull effect, and the variation about it, is adjusted, as if the population density was constant (set to the mean of the DMAs). Likewise, the estimated slope of the density-dependent effect is adjusted as if the percentage cull was constant in all DMAs.

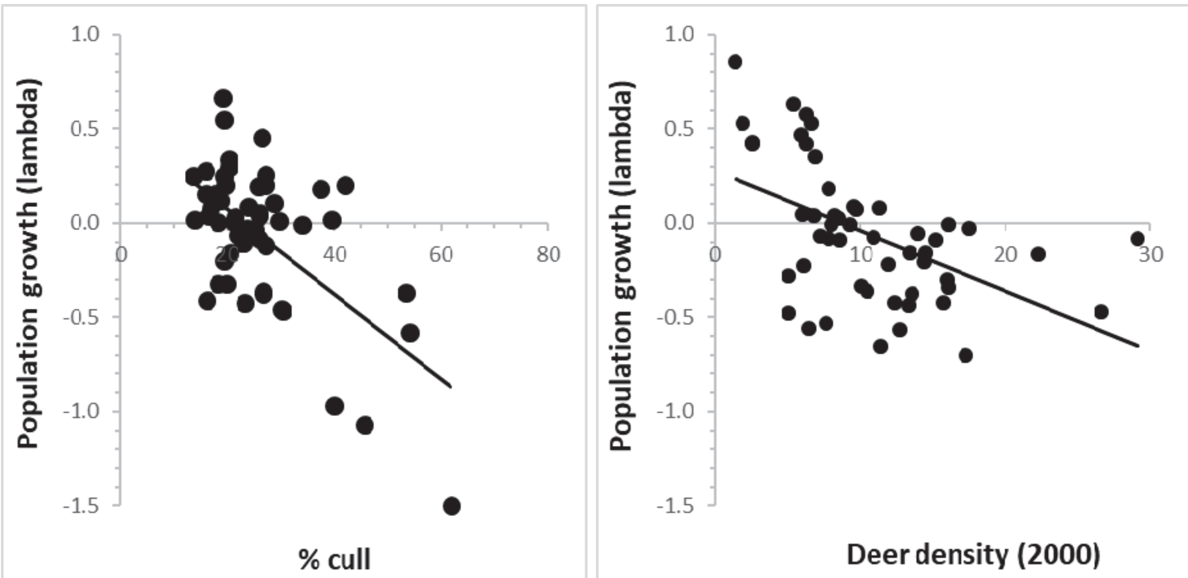

Figure 12: Population growth (Log 2019 density – Log 2000 density) in 52 DMAs, plotted against the mean percentage cull (left-hand panel), and population density estimate in 2000 (right-hand panel). In each plot the points and slope are adjusted for the other explanatory variable.

3.3 Variation in sheep stocks

3.3.1 Overall trends in sheep densities

Sheep stocks have declined across much of Scotland, in particular, in the North and West Highlands (SAC 2008, Thomson 2011). Across the Highland & Island region numbers have declined 40%, from around 65 ewes km^2 in the early 1990s to around 40 ewes km^2, recently (Figure 13). Because, there is no distinction between sheep on the open-hill and in the in-bye fields, changes on hill-ground may be even greater. However, we could find no evidence that these gross changes had any influence on the overall trend in red deer density, and recently deer have ceased increasing despite the substantial decline in competition from sheep.

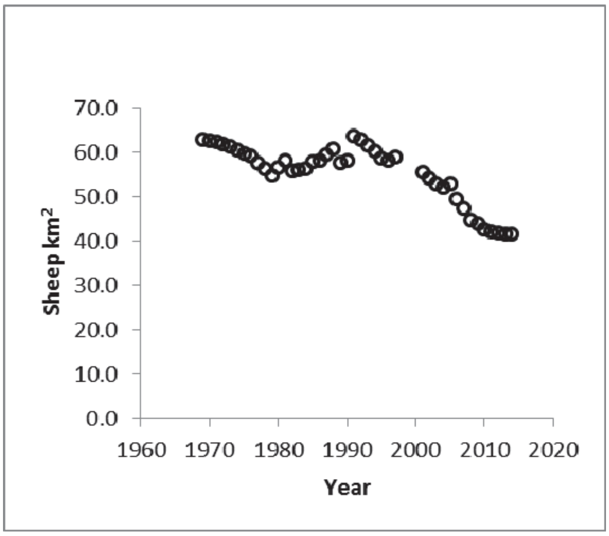

Figure 13: Trend in sheep density (ewes km^2) across the Highlands and Islands (1969–2015).

3.3.2 Regional variation in sheep density and impact on deer densities across Scotland

Although there was no sheep density data available after 2015, we repeated our earlier regional analysis (Albon *et al.,* 2017) since we had new estimates of recent deer densities in ten DMAs not previously available. However, as before we could find no evidence for a relationship between either spatial deer density or change in deer density (2000-2019) and either mean sheep density (1999 -2015), or relative change in sheep stocks. Nor was there any evidence for relationship between deer density and sheep stock dynamics after accounting for the level of culling and density dependence (see Table 1, Figure 12 above). The apparent lack of impact of differences in sheep stocks at the scale of DMA may be partly because of a positive spatial correlation between the %cull and mean sheep density ($r = 0.387$, $P < 0.005$), and partly because the real variation in sheep density is at the smaller spatial scale of differences between Deer Management Units within DMAs (see below). Although Albon *et al* 2017 found evidence of a negative effect of higher sheep stocks on deer density at the level of the parish, this was not re-investigated here because of lack of time and the fact that there were no estimates of sheep density beyond 2015.

4. CONCLUSIONS AND FUTURE DIRECTIONS

4.1 Conclusions

Variation in cull rate (% of the counted population) is a major factor influencing the variation in population growth rate between Deer Management Areas over the last two decades. In general, culls of less than 22% are likely to see populations rise, whereas higher culls will depress numbers. Management intervention culls designed to reduce numbers in areas such as Cairngorm/Speyside and East Grampian – Glen Isla/Glenshee have seen reductions of density by as much as 30%. DMAs with higher densities also tended to have lower intrinsic growth rates because recruitment (calf:hind ratio) declines with rising density.

As reported previously (Albon *et al.,* 2017) the mean density of deer across the Highlands and Islands of Scotland of deer peaked in 2000. Estimates for 2017, 2018 and 2019 confirms the population is stable at just under 10 deer km^2. The cessation of rising density can be accounted for by the fact that the total cull has increased steadily since the 1960s to a peak around 2000, and recently, of c.2.25 deer km^2. Thus, given the mean density of deer is currently estimated about 9.5 deer km^2, these cull rates are slightly higher than the 22% which in general across the DMAs tends to drive population decline. This could account for the apparent downward trend (9% fall) in deer density over the last 20 years. Furthermore, the fact that the cull of calves has increased disproportionately from almost zero in the early 1960's to c.35 calves shot per 100 hinds shot in the last ten years, would reinforce the downward trend because there are fewer calves to recruit (even after allowing for the density-dependence associated with higher population densities).

4.2 Future directions & recommendations

First, deer managers who want to have stable populations will need to cull at around 22% rather than the traditional 1/6th: those with comparatively low-density deer populations with high calf:hind ratios will need to shoot proportionally more. Second, although there was a record cull in 2017/18, the cull of deer km^2 was falling year on year over the previous 20 years, faster than the downward trend in deer density estimated from the counts, so effort to maintain the cull should be a priority. Third, SNH should try to establish a more consistent cull return policy. Fourth, the ability to detect changes in deer density is compromised by the comparatively large confidence intervals on the estimates. The power to detect change could be improved by more regular censuses, of sub-samples of DMUs, in a systematic rolling programme across the DMAs. Sample designs suggested in previous contracts (Albon *et al.,* 2009; 2011) could be trialled to measure the effectiveness of such schemes.

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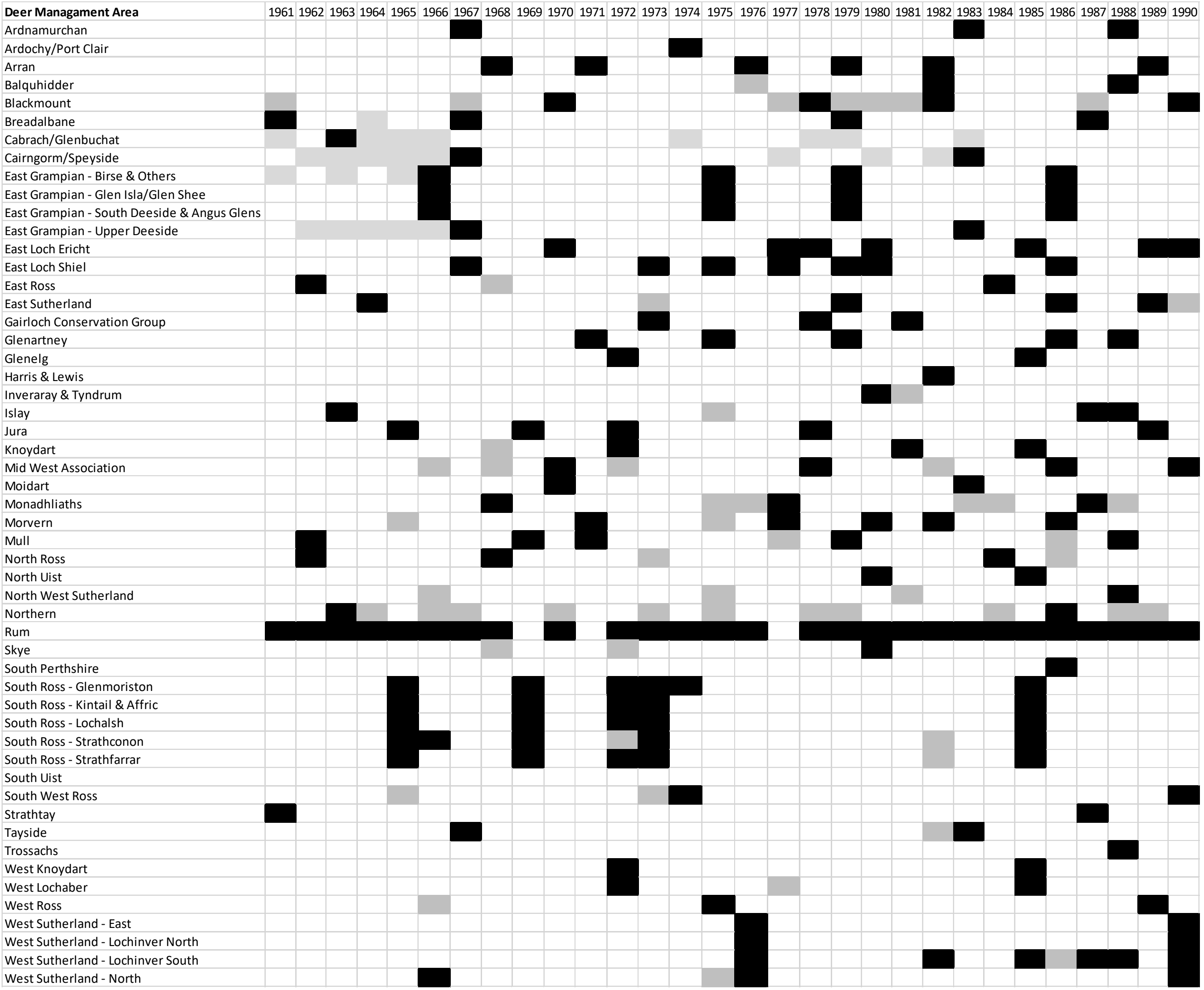
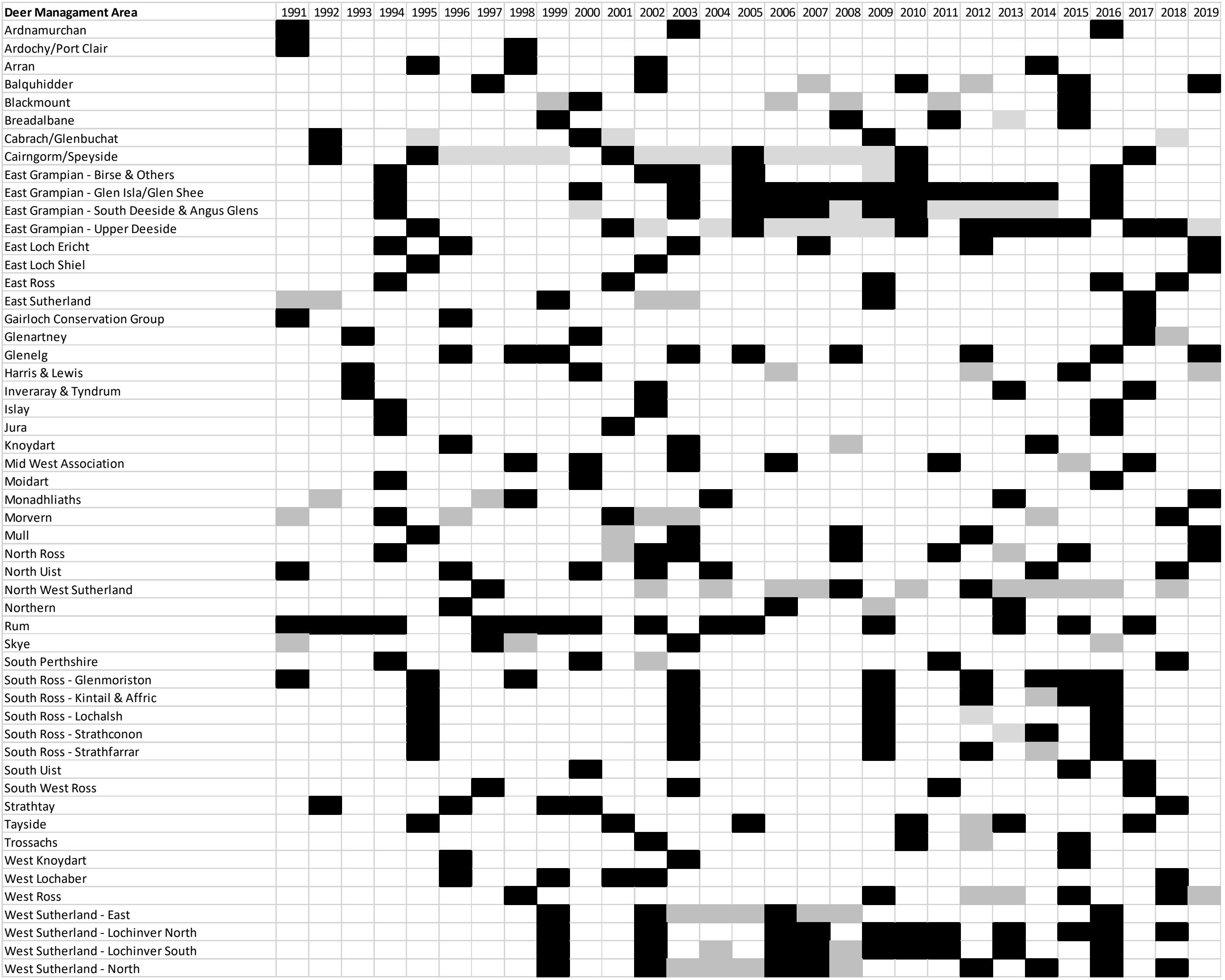
ANNEX 1: THE DISTRIBUTION OF COUNT DATA BY DEER MANAGEMENT AREA AND YEAR SINCE 1961 PART A 1961-1990



Black squares >50% of the DMUs in the DMA counted. Grey blocks less than 50% counted.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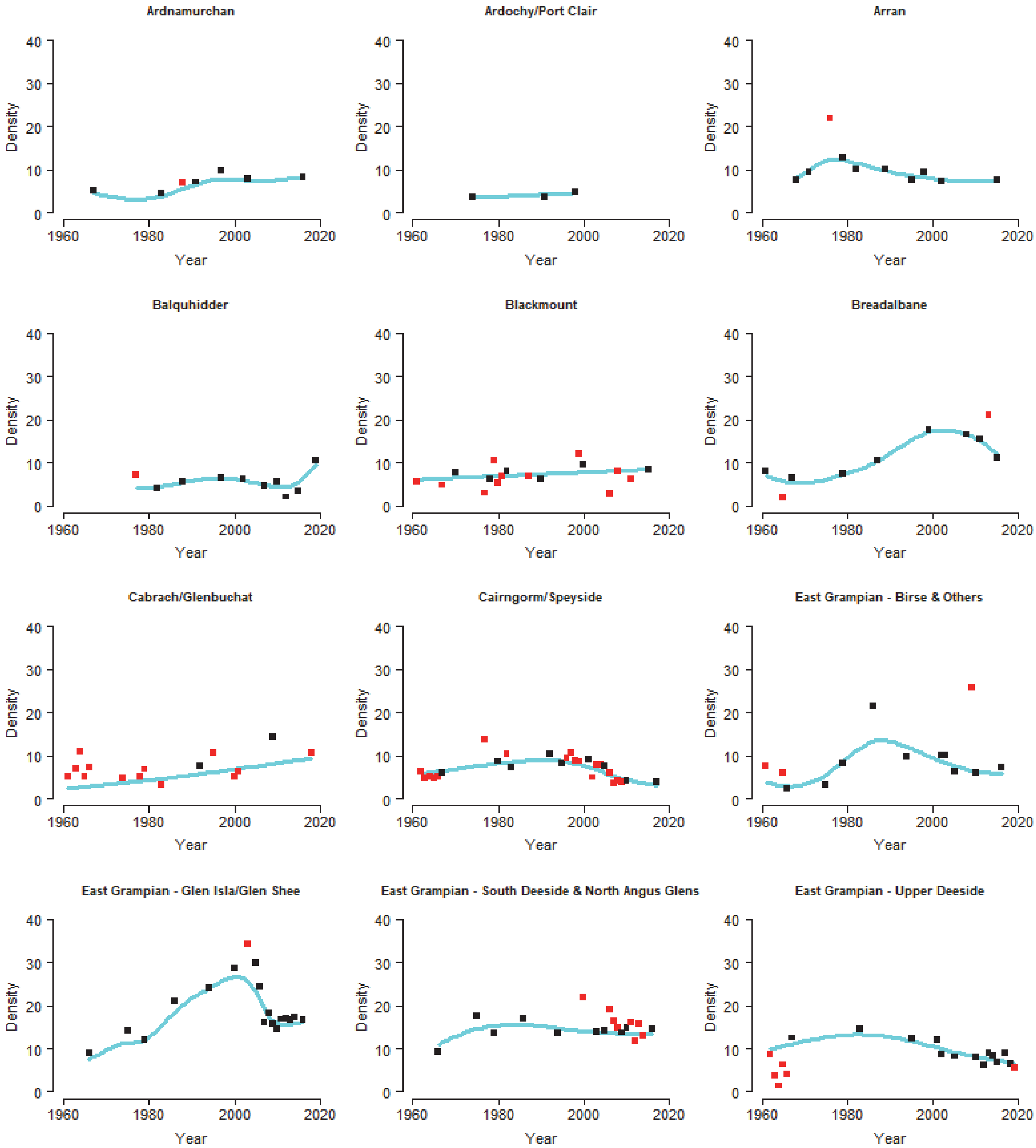
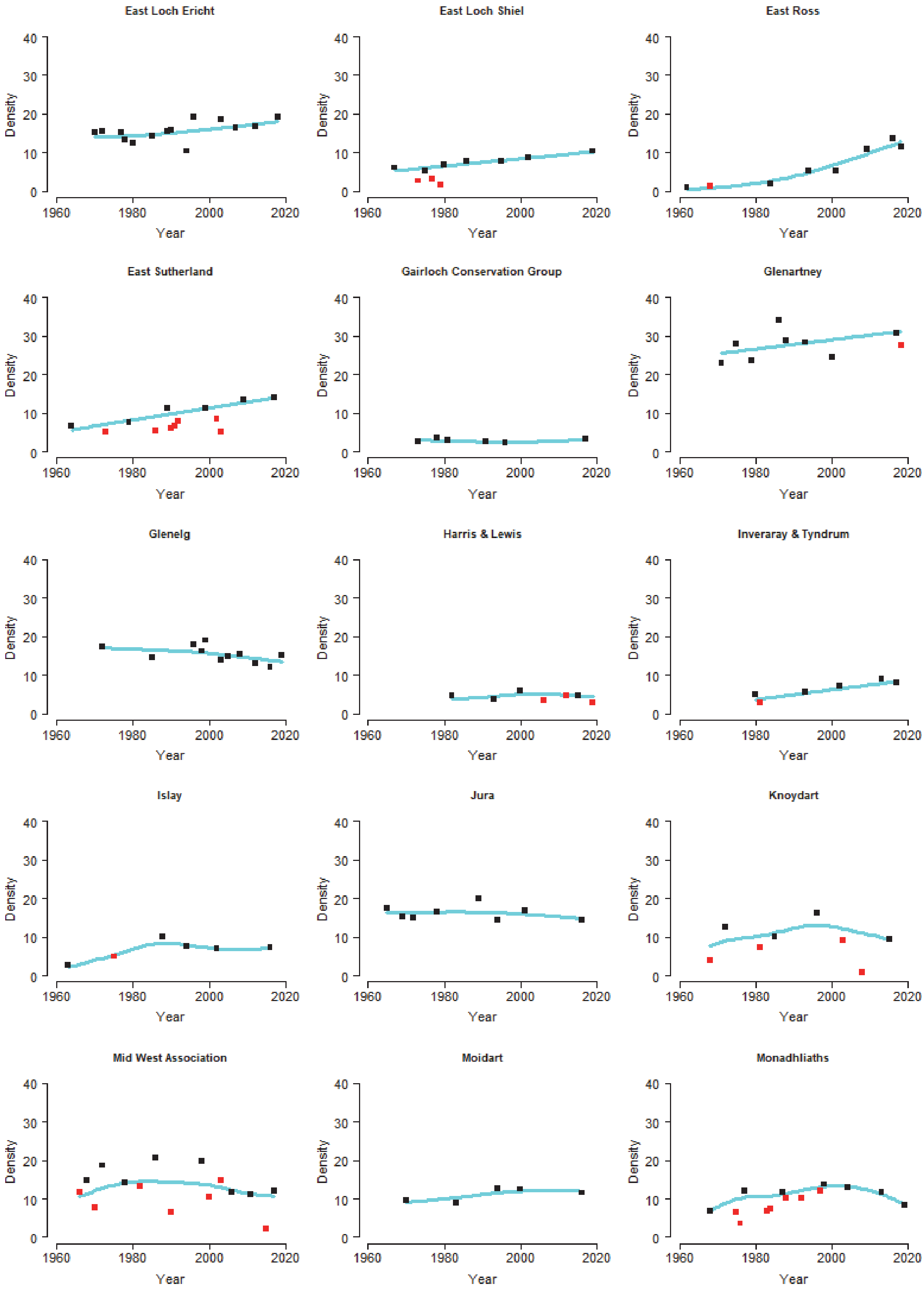
Ardnamurchan
Ardochy/Port Clair
Arran
Balquhidder
Blackmount
Breadalbane
Cabrach/Glenbuchat
Cairngorm/Speyside
East Grampian - Birse & Others
East Grampian - Glen Isla/Glen Shee
East Grampian - South Deeside & Angus Glens
East Grampian - Upper Deeside
East Loch Ericht
East Loch Shiel
East Ross
East Sutherland
Gairloch Conservation Group
Glenartney
Glenelg
Harris & Lewis
Inveraray & Tyndrum
Islay
Jura
Knoydart
Mid West Association
Moidart
Monadhliaths
Morvern
Mull
North Ross
North Uist
North West Sutherland
Northern
Rum
Skye
South Perthshire
South Ross - Glenmoriston
South Ross - Kintail & Affric
South Ross - Lochalsh
South Ross - Strathconon
South Ross - Strathfarrar
South Uist
South West Ross
Strathtay
Tayside
Trossachs
West Knoydart
West Lochaber
West Ross
West Sutherland - East
West Sutherland - Lochinver North
West Sutherland - Lochinver South
West Sutherland - North

ANNEX 2: THE DEER MANAGEMENT AREA TRENDS IN DEER DENSITY

Plots of estimated deer density against year in each Deer Management Areas in alphabetical order. Black squares are where more than 50% of the DMUs were counted. Red squares are where less than 50% of DMUs were counted. The blue lines are the fitted GAMs through the points as described in Box 2.




East Loch Ericht
East Loch Shiel
East Ross
East Sutherland
Gairloch Conservation Group
Glenartney
Glenelg
Harris & Lewis
Inveraray & Tyndrum
Islay
Jura
Knoydart
Mid West Association
Moidart
Monadhliaths
Density
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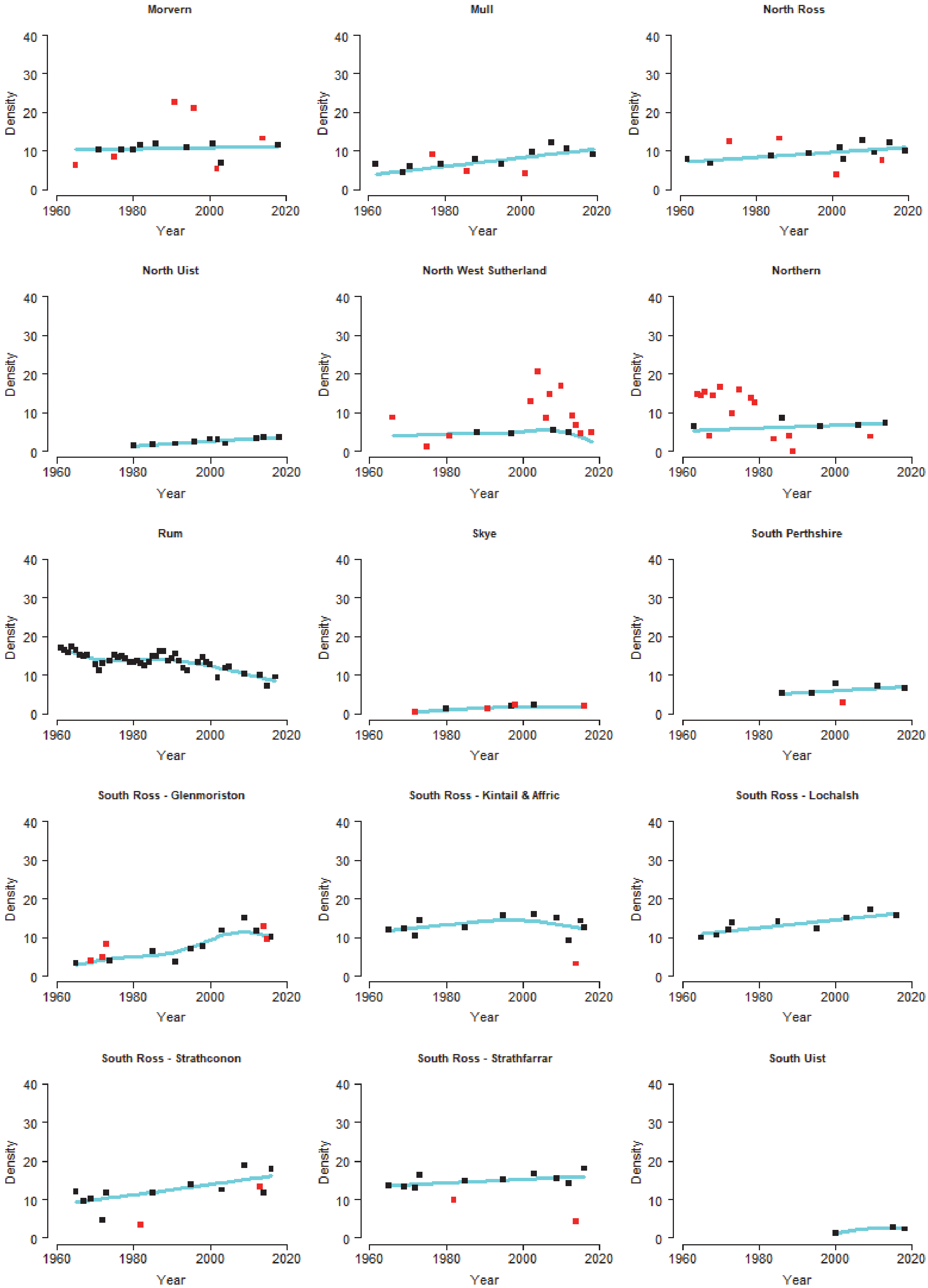
Morvern
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North Uist
North West Sutherland
Northern
Rum
Skye
South Perthshire
South Ross - Glenmoriston
South Ross - Kintail & Affric
South Ross - Lochalsh
South Ross - Strathconon
South Ross - Strathfarrar
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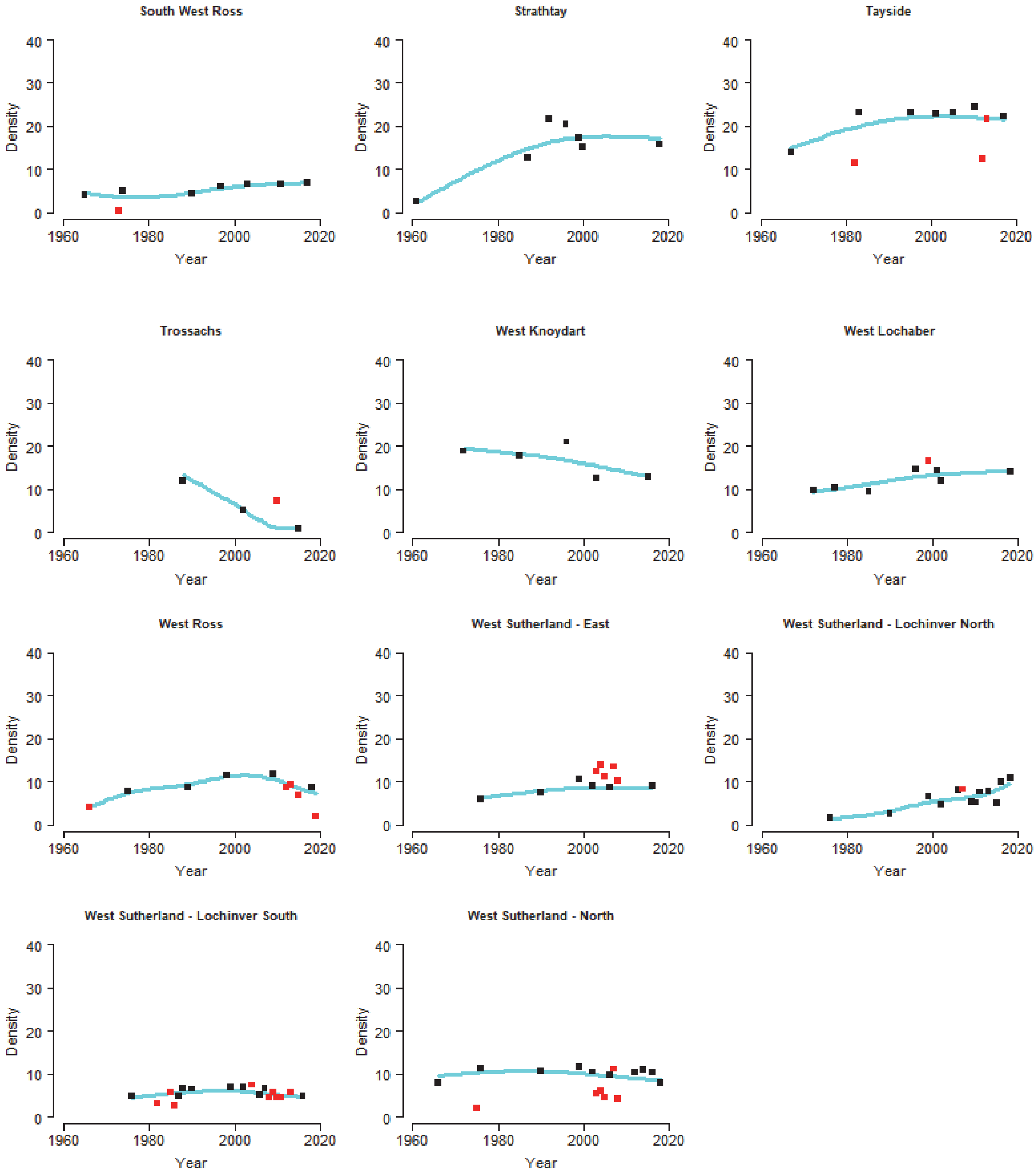
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West Sutherland - North
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