

PAST AND FUTURE MASS MORTALITIES OF THE SAIGA ANTELOPE:

REMOTE ANALYSES OF RECENT HUMAN-MEDIATED DIE-OFFS

by

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Abstract

Mass mortalities limit the viability of mammal populations; particularly those of endangered species with reduced population sizes. Die-offs of the Critically Endangered saiga antelope (*Saiga tatarica*) were reported in 2010 and 2011, post-calving. The current but untested hypothesis is that a combination of unusual weather, topography and pasture improvement resulted in fast-growing, moist and atypically-composed forage, which caused a form of metabolite toxicosis. An analysis of assumptions underlying this hypothesis using meteorological data and satellite imagery revealed that neither temporal variation in weather nor highly-productive, moist forage are likely to have been factors in the die-offs; although significantly lower vegetation or soil moisture in die-off zones than in the surrounding landscape indicates events were location-dependent, and therefore precipitated by changes in calving site selection driven by human environmental perturbations. Unusual topography and pasture improvement in these locations probably promoted legume-rich pastures which triggered a condition more closely related to bloat, although variables may be acting at scales finer than assessed, signifying a need for local assessment of die-off pastures and demarcation of similar areas. High natural mortality during saiga calving with various aetiologies indicates an urgent need to limit disturbance at this vulnerable time and increase population sizes to prevent local extirpation.

'Sed primo parcius praebenda est nouitas pabuli, inflat enim...'

'But new provender is at first to be administered very sparingly, for it bloats up... [the cattle]'

(Palladius, 4th century AD; in reference to the effect of early growth alfalfa on livestock)

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I. Introduction

(1) Mass mortalities

Mass mortalities are increasingly recognised as a significant limitation to the long-term viability of terrestrial mammal populations (Lande *et al.*, 2003). The occurrence of extreme natural events, such as disease epidemics or droughts, substantially increases minimum viable population size (Mangel & Tier, 1993). In combination with increasing indirect anthropogenic pressures these events represent an important challenge for conservation (Ameca y Juarez *et al.*, 2012). Projected increases in global surface temperatures and more variable precipitation (IPCC, 2007) are likely to increase the incidence of climatically driven events. The effects and incidence of disease are also amplified by human activities, for example, through habitat fragmentation, population isolation and increasing proximity with livestock (Scott, 1988); by altering habitats and causing shifts in population distribution we are providing opportunities for new diseases to arise in populations or modifying the epidemiology of existing syndromes (Deem *et al.*, 2001).

Natural die-offs of large mammalian herbivores, ungulates in particular, dominate the literature; and mortality events are most frequently recorded in semiarid ecosystems (Young, 1994). The former are often food limited and consequently subject to environmental fluctuations; the latter often support large populations whilst being prone to extremely dry periods. The saiga antelope (*Saiga tatarica*), a nomadic ungulate of the arid and semiarid ecosystems of Central Asia (Bekenov *et al.*, 1998), is an archetypal example of a species at threat from mass mortalities. The saiga has been subject to large fluctuations in population size over the past century as a result of biotic, abiotic and anthropogenic factors that have changed in ascendance through time (Robinson & Milner-Gulland, 2003); and is now at extremely high risk of extinction in the wild (IUCN, 2008).

(2) Recent and past mortality events of the saiga antelope

Recent years have seen mass die-offs of the saiga reported in the Ural population in Borsy, Western Kazakhstan in 2010 (~12,000 to 15,000 individuals (Kock *et al.*, 2012)) and 2011 (400+ individuals (Kazakhstan Today, 2011)). An initial diagnosis of pasteurellosis, an opportunistic infection caused by bacteria naturally present in many mammals, is now considered unreliable (Kock *et al.*, 2012). Post-hoc analyses of the events in 2010 and 2011 suggest that, rather than being caused by an infectious pathogen, the mortalities may be associated with the attributes of the pastures upon which the saigas were grazing (Sapanov, 2011; Kock *et al.*, 2012).

A number of mass mortalities throughout the past century have also been ascribed to pasteurellosis, for example, in the Betpak-Dala population in 1981 and 1988 (70,000 and 270,000 individuals, respectively (Fadeev & Sludskii, 1982; Khakin & Sedov, 1992)) and in the Ural population in 1984 (100,000

individuals (Fadeev, 1986)); although these diagnoses have also been disputed (Lundervold, 2001). The bacteria responsible, of the genus *Pasteurella*, are naturally found on mammalian mucosal surfaces (Kuhnert & Henrik Christensen, 2008) and have been isolated post-mortem from the lungs of healthy saigas (Lundervold, 2001). Consequently, in sheep, stress is an important factor in opportunistic infection which is largely a juvenile affliction (Kahn, 2005).

(3) Current hypothesis

The current hypothesis is that pastures upon which saigas were feeding immediately prior to the mortality events were, in comparison to typical pastures (Sapanov, 2011; Kock *et al.*, 2012; Fig. 1):

- i) Unusually nutrient-rich and fast-growing.
- ii) Abnormally high in moisture content.
- iii) Atypical in plant species composition.

As a result of one or more of the following factors:

- a) Die-off zone topography; located in surface-depressions which are naturally more fertile and accumulate moisture.
- b/c) Unusually warm and/or wet weather prior to and during the events.
- d) Regular cutting and/or seeding for hay-making; possibly favouring annual grasses over perennials.

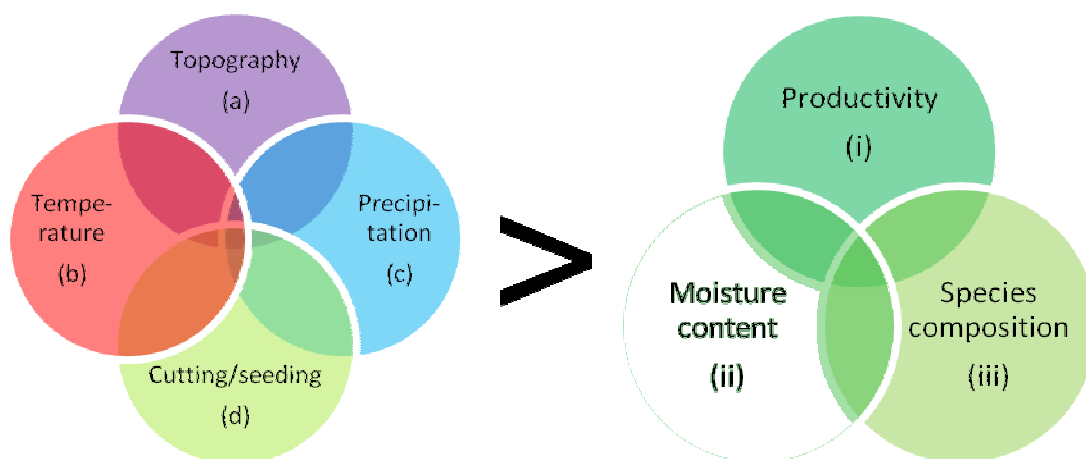


Figure 1. Current hypothesis for saiga mass mortality events in 2010/11. A combination of one or more unusual environmental factors (topography of the die-off zones (a); temperature (b) and/or precipitation (c) during and prior to the events; and cutting and/or seeding for hay-making) promoted one or more atypical pasture attributes (plant productivity (i), moisture content (ii) and/or species composition (iii)) (Sapanov, 2011; Kock *et al.*, 2012).

Consumption of this vegetation is hypothesised to have led to a form of atypical interstitial bronchopneumonia (AIP; Kock *et al.*, 2012); a disease characterised by extreme ruminal dysfunction which is common in cattle (Cheng *et al.*, 1998) but hitherto undescribed in the saiga antelope. Certain forms of forage or feed trigger the dysfunction which causes bloating and respiratory problems and can lead to asphyxia, with high levels of recorded mortality (Kahn, 2005); Fig. 2).



Figure 2. Dead saiga females in Borsy, West Kazakhstan, May 2010. Abdominal swelling may be a combination of pre-death rapid-onset pasture bloat and post-death decomposition. Photo by Republic KZ News.

(4) The problem

These analyses were based on expert opinion, anecdotal evidence, local observations in September 2011 and a limited weather assessment. Whilst there is an *a priori* argument for the above hypothesis, based on similar syndromes in other ruminants, the underlying assumptions have yet to be proven.

There is however a critical need to establish the aetiology of these events. Recent range-wide saiga population assessments established a total population of ~105,000 (CMS, 2010); a 90% reduction in < 20 years (Milner-Gulland *et al.* 2001). Although large fluctuations have characterised saiga populations historically, and high saiga population growth rates allow fast recovery from steep declines (Bekenov *et al.*, 1998), low current individual population sizes relative to the magnitude of recent mortality events indicate an urgent need to forestall further events to prevent future local extirpation. This need is recognised in international legislation; impact assessment of natural threats such as disease and climate change is listed as a priority activity in the Convention on Migratory Species saiga conservation action plan (CMS, 2006).

(5) Aims and objectives

A comprehensive retrospective analysis addressing all assumptions underlying the current hypothesis would involve local assessment of pasture attributes proximal in time to the events. As logistical

constraints precluded local data collection this research project aimed to explore some, but not all, of the assumptions underlying the hypothesis, using remotely-available data.

Specifically, I sought to establish:

1. Whether temperature (Fig. 1b) and/or precipitation (Fig. 1c) prior to the events in 2010 and 2011, in the vicinity of the mortality events, departed significantly from long-term variation for that time of year, using freely-available meteorological data.
2. Whether plant productivity (Fig. 1i) and/or moisture content (Fig. 1ii) in the die-off zones, during the events, departed significantly from long-term variation for those locations at that time of year, and also from the surrounding landscape, using satellite imagery.
3. Whether any variation in weather or vegetation found in relation to the 2010/11 mortality events correlated with similar variations in the same characteristics surrounding events in the 1980s, in order to explore the possibility that historical die-offs previously diagnosed as pasteurellosis could also be ascribed to the causes outlined above.

II. Methods

(1) Mortality events

The mortality events in 2010 and 2011 took place in overlapping locations, approximately 80 km² and 60 km² in area, respectively, within the Ural saiga population in the far west of Kazakhstan (Kock *et al.*, 2012; Fig. 3; latitude/longitude of centre point: 50.1115°, 47.5559°; all geographic coordinates in report text in decimal degrees).

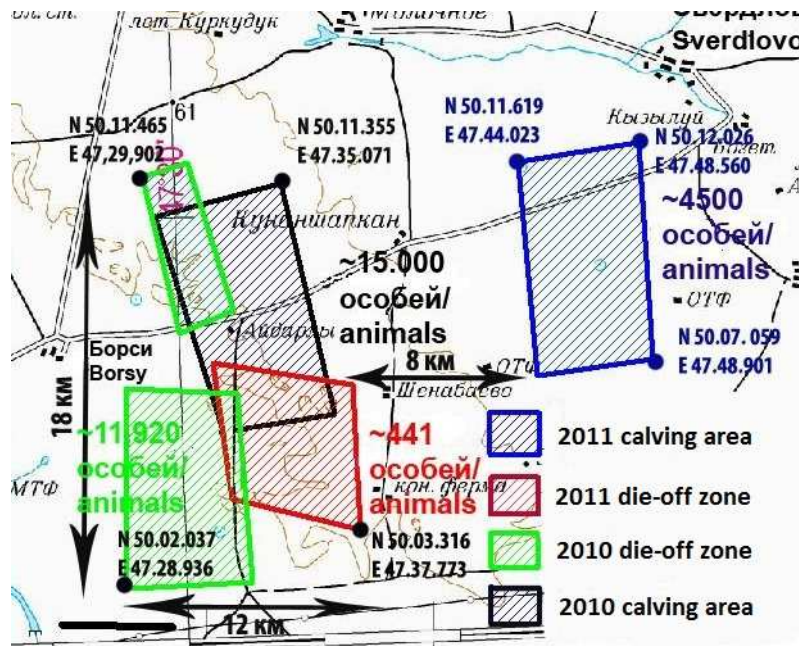


Figure 3. Die-off zones in 2010 (green hatching) and 2011 (red hatching), in comparison to calving areas (black and blue hatching, respectively). Number of deaths in die-off zones/animals in calving areas shown in corresponding colour. Modified from Kock *et al.* (2012).

2010/11 event patterns were comparable in all but magnitude: post-calving, large numbers of mainly female and juvenile saigas moved to new pastures; within a few days high proportions of adult saigas began dying, with lactation-dependent calves expiring later; total mortality rates in affected areas were ~ 75%. Calving in 2010 took place on 1st to 13th May, with deaths occurring on 18th to 21st May. Saigas left calving areas slightly later in 2011, 18th to 19th May, with deaths occurring on 26th to 27th May. Although mortality sites were within the Ural saiga population's range, calving grounds were considerably further north than in previous years (Fig. 4), in line with recent changes in calving ground selection (Singh *et al.*, 2010a).

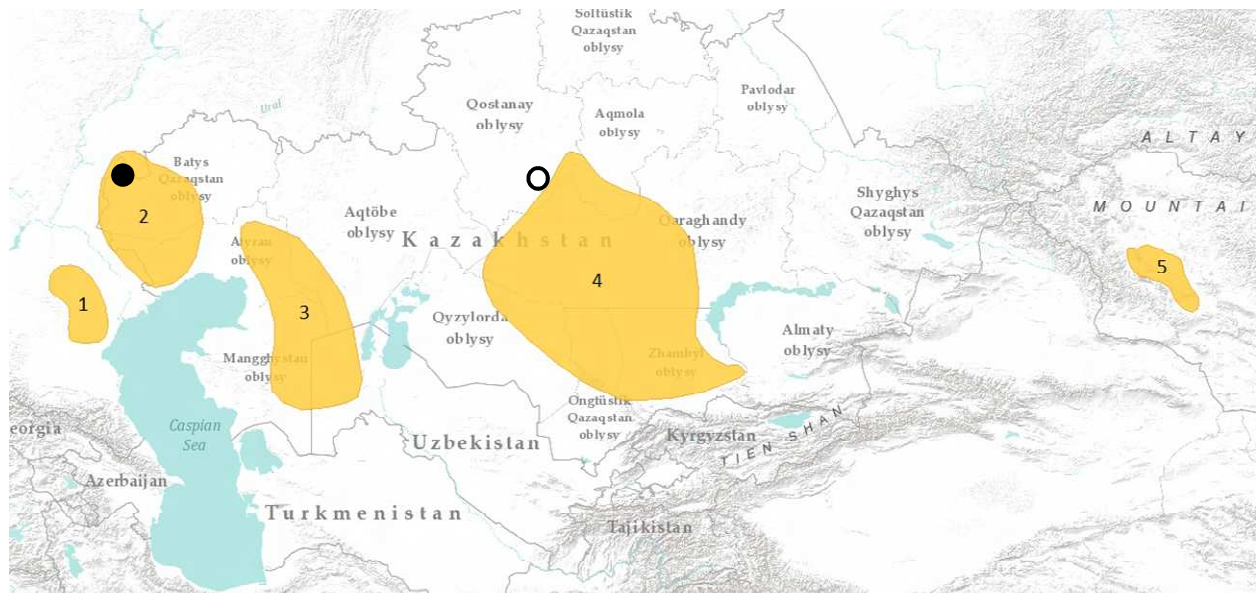


Figure 4. Saiga tatarica geographic range by population (1. Pre-Caspian population, 2. Ural population, 3. Ustiurt population, 4. Betpak-dala population, 5. Mongolian population) and mortality event epicentres in 2010/11 (●) and 1988 (○) (Reproduced from: Turgai Regional Executive Committee, 1988; Milner-Gulland *et al.*, 2001; IUCN, 2008; and Kock *et al.*, 2012).

Circumstances surrounding earlier pasteurellosis-ascribed events were less well-documented. Events in 1981 and 1988 took place in Turgai province (500,000 km²), also in May, with similarly high female and calf mortality (Fadeev & Sludskii, 1982; Khakin & Sedov 1992). The 1984 event took place in February/March between the Volga and Ural rivers (Fadeev, 1986); a description which encompasses event sites in 2010/11 but is a minimum of 400km in breadth, with different mortality patterns.

The paucity of available literature and the requirement for precise event coordinates limited analysis of historical die-offs to the 1988 event exclusively. An official report describes deaths taking place during the Betpak-Dala population's calving period over a wide area centred on 49.6541°, 65.6338° (Turgai Regional Executive Committee, 1988; Fig. 2). Similarly to recent events, this point is in the north-west extreme of the population's range (Fig. 4). Whilst sufficient for a comparison of weather patterns with recent events; lack of fine-scale data regarding die-off areas precluded imagery-based vegetation analysis.

(2) Study sites

The 2010/11 and 1988 event sites are situated at similar latitudes (~50°). Annual precipitation is higher in this steppe zone in comparison to the semi-desert and desert zones further south in the saiga's distribution (>300 mm, 200 to 250 mm and <200 mm, respectively; Singh *et al.*, 2010b). All three zones share an extreme continental climate, typified by hot, dry summers and severe winters, and a flat topography. Plant productivity and composition in semi-arid ecosystems are principally determined by precipitation amount, seasonality and frequency (Noy-Meier, 1973). Saigas migrate on a seasonal basis

from winter ranges in the southern desert zone to summer ranges in the northern steppe zone driven by changes in productivity (Singh *et al.*, 2010b); pausing to calve mid-range en route. Steppe zone plant communities are grass-dominated and growth is strongly seasonal. Nutrient rich and moist depressions may contain higher concentrations of legumes and shrubs (Sapanov 2011).

(3) Weather data

i) Collection

In order to test the hypothesis that weather variables during and prior to the events departed significantly from long-term variation data were required with high spatial and temporal resolution: although data would not be available for precise event locations they should be representative to allow the articulation of location-dependent conclusions; with frequent measurements, to allow the identification of meaningful deviations; forming a consistent and continuous historical time-series, to establish representative conditions, up to the time of the events.

Four potential interpolated and meteorological station-derived weather data sources were reviewed accordingly, including the CRU TS 2.0 (Mitchell *et al.*, 2004) and WorldClim (Hijmans *et al.* 2005) gridded data sets, neither of which proved satisfactory. Further assessment identified products derived from the Global Historical Climatology Network data set (NCDC, 2012); including the GHCN-Daily database of daily measurements from 75,000 worldwide meteorological stations and related GHCN-monthly version 2 and 3 databases of monthly mean temperature and precipitation, respectively. All have undergone quality controls for duplications, inconsistencies and outliers, but data from individual stations vary in length and consistency. Although it would not be possible to interpolate precise conditions for event sites using these data an assumption was made that concurrent weather patterns from a number of proximal surrounding stations could be used as a proxy.

ii) Analysis

Global meteorological data sets were downloaded and imported into Microsoft Excel for collation and analysis. Stations were categorised according to distance from event sites using geographical coordinates to calculate great-circle distances using the Haversine formula (Sinnott, 1984). A subset of stations within 300 km of event sites was reviewed for length and consistency according to World Meteorological Organization guidelines (WMO, 2007). Consecutive records over 30 years are considered sufficient to calculate WMO-defined 'climate normals' (means) which eliminate year to year variations but are representative (WMO, 2007). The WMO also recommends a '3 and 5' rule for missing temperature data quality control, in which a data set from which any 30-year average is derived should not contain a total of 5 missing years or 3 consecutive years (WMO, 2007). Precipitation totals necessitate no missing data.

30-year climate normals for the period 1980 to 2009, and 1958 to 1987 were constructed for comparison with 2010/11 and 1988 events, respectively, calculated as the 30-year mean (\pm standard deviation) of a given element: preferentially from a series of corresponding annual dekadal temperature averages or precipitation totals, if daily measurements were available; or from monthly averages otherwise. Normals for January through May were plotted next to corresponding event year elements on line or bar graphs, for temperature and precipitation data, respectively, for visual comparison. The analysis encompassed both spring growing season and winter months as winter precipitation in semiarid environments is less likely to evaporate, and so exerts a strong influence on plant growth dynamics (Schwinning *et al.*, 2003).

(4) Satellite imagery

Remote sensing imagery provides the means for convenient, inexpensive and systematic analysis of changes in vegetation (Xie *et al.*, 2008). A number of optical satellite systems provide earth observations useful in vegetation image processing, including the NOAA-AVHRR, the Terra and Aqua satellite born Moderate-resolution Imaging Spectroradiometer (MODIS), and the SPOT satellite (Jung *et al.* 2006). All provide a suite of surface reflectance products with differing degrees of processing, spatial resolution and temporal granularity. The MODIS level-3 datasets (level denoting data has been mapped and gridded with defined accuracy/quality assurance) were chosen on the basis of ease of access and support provided (LP DAAC, 2012). The MOD13Q1 data set provided a set of global surface layers for vegetation analysis at 250 m resolution for 16 day periods from 2000 to present.

i) Vegetation indices

Indices which mathematically transform satellite-derived surface reflectance at two or more wavelengths into quantitative vegetation measures have been used to assess temporal and spatial variation, particularly in arid and semiarid ecosystems with relatively low plant cover (Chen *et al.* 1998). A review of the literature revealed over 150 different potential vegetation indices. Two were chosen for implementation: the Normalized Difference Vegetation Index (NDVI), a well studied and widely used index available as a pre-processed MODIS product; and the Normalized Difference Water Index (NDWI).

NDVI was selected to assess if vegetation productivity in die-off zones during the events varied from averages over the last decade, and from the surrounding landscape. Although more directly a measure of plant density NDVI is also a useful proxy for productivity (Paruelo *et al.*, 1999). NDWI was selected to assess variations over the same spectrum in leaf water content and soil moisture, as forage moisture content was conjectured to be an important factor in ruminal dysfunction (Sapanov, 2011). NDWI is also easily calculated using reflectance bands available in the same MODIS data set as the NDVI layer, using the formula elucidated by Gao (1996): $NDWI = (pNIR - pSWIR) / (pNIR + pSWIR)$, where pNIR and pSWIR

are reflectances at Near-infrared and Short-wavelength infrared, corresponding to MODIS bands 2 (841–876 nm) and 7 (2105–2155 nm), respectively. MODIS bands 5, 6 and 7 all represent SWIR wavelengths; however band 7 responds strongest to dry soil conditions (Wang *et al.*, 2008).

ii) Data collection

10 by 10 arcdegree-tiles corresponding to the die-off region were calculated (h21v04 and h21v03). HDF-EOS format image tiles from 2000 to 2011 for the 16-day period closest to the die-off dates in 2010 and 2011 (ending Julian date 129 and 145, respectively) were downloaded via file transfer protocol software. Image reprojection from native sinusoidal state to geographic projection, sampling of data for subset area of interest using geographic coordinates, selection of NDVI, band 2 and band 7 layers, mosaicking back into single image (for spatial analysis), and conversion into GeoTIFF layers, were all completed using the MODIS Reprojection Tool (LP DAAC, 2011). Data were subsequently visualised, pseudo-coloured (NDVI only) and extracted using ArcGIS (ESRI, 2010), before statistical analysis and graphical representation using the R software environment (R Development Core Team, 2012).

iii) Temporal analysis

NDVI, band 2 and band 7 pixel values were extracted for die-off zones in each period and NDWI computed. Mean annual NDVI and NDWI values (\pm standard deviation) were calculated for die-off periods in 2010 (late April/early May), and 2011 (late May), for comparison. Values were plotted as a function of year and period in a combination box plot for visual assessment.

iv) Spatial Analysis

To assess whether vegetation in die-off zones departed significantly from variation in the surrounding landscape NDVI values were extracted and NDWI values calculated from pixels in a 50x50 km square surrounding the zones. A two sample t-test was used to compare mean NDVI and NDWI for die-off zones with the surrounding landscape in 2010 and 2011 (significance at $p = 0.05$). Data were represented in violin plots, a derivation of the boxplot useful for visualising large data set distribution, using the R vioplot package (Adler, 2005).

(5) Note on statistical analysis

Whilst a Student's t-test is normally appropriate for the comparison of means it is not suitable for the comparison of serially correlated data, such as meteorological measurements (Zwiers & Storch, 1995); or of other characteristics of a single location through time e.g. vegetative characteristics. T-test comparisons of serially correlated data will usually be liberal in their finding of significance.

Furthermore, although linear regression models are frequently applied to ecological data, they are not always appropriate (Zuur *et al.*, 2009). Resolving such issues of auto-correlation has been described as

'non-trivial' (Storch & Zwiers, 2001, p.114). Whilst not insurmountable, time and resource constraints prohibited resolution of these issues within the bounds of this research. Consequently, formal statistical comparison of mean weather and vegetation index data with long-term variation was not possible. A number of methods for accounting for autocorrelation could have been reviewed had more time been available, for example, the calculation of equivalent sample sizes which make the normal t-test more conservative, or via the use of the 'table-look-up-test' (Storch & Zwiers, 2001). A mixed effects model which accounted for temporal dependence between observations would have been the optimal solution; however selection and implementation of appropriate models requires substantial consideration (Zuur *et al.*, 2009).

III. Results

(1) Weather

Of over 40 meteorological stations assessed, 3 within 300 km of the 2010/11 event epicentres provided usable temperature data, although all were located east; situated in the localities of Aleksandrov-Gaj, Russia, and Furmanovo and Uralsk in Kazakhstan (80, 155 and 300 km distant, respectively; Fig. 5). Aleksandrov-Gaj alone yielded precipitation data necessitating an extension of search parameters to include a station in Astrakhan, Russia (429 km). Similarly, 3 stations within 300 km of the 1988 event epicentre provided temperature data; situated in Turgaj, Karsakpaj and Zhezkazgan, Kazakhstan (154, 219 and 232 km distant, respectively; Fig. 6). Only Turgaj and Zhezkazgan provided precipitation data requiring inclusion of Kustanay, Kazakhstan (420 km). Long-term weather patterns observed in the vicinity of both event sites were representative of semi-arid climate systems: low variability in temperature and extremely high variability in precipitation (Noy-Meir, 1973).

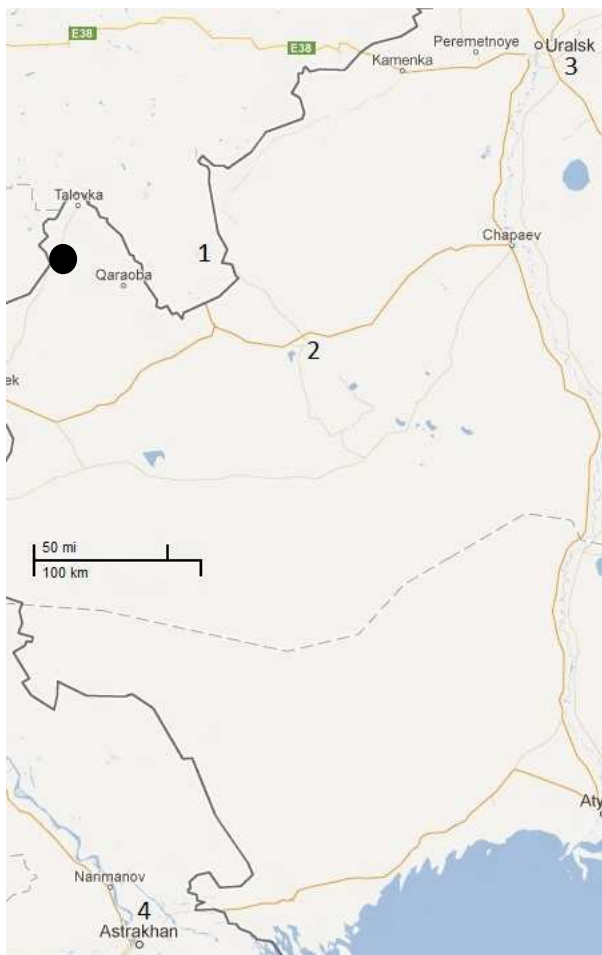


Figure 5. Distribution of meteorological stations with respect to mortality event epicentres in 2010/11 (●), station elevation in brackets: 1. Aleksandrov-Gaj, Russia (23 m); 2. Furmanovo, Kazakhstan (10 m); 3. Uralsk, Kazakhstan (37 m); 4. Astrakhan, Russia (-22 m).

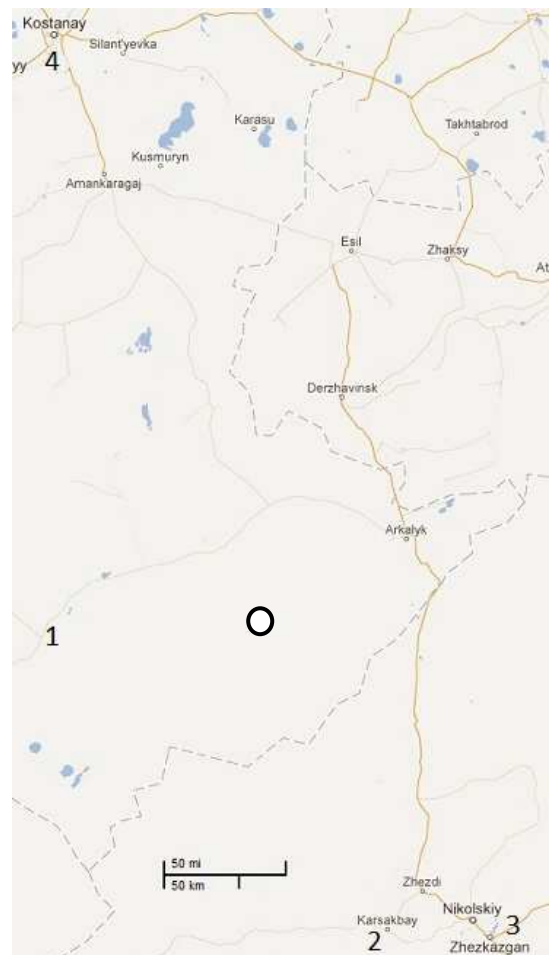


Figure 6. Distribution of meteorological stations with respect to mortality event epicentre in 1988 (○), station elevation in brackets: 1. Turgaj (124 m); 2. Karsakpaj (214 m); 3. Zhezkazgan (346 m); 4. Kustanay (169 m; all in Kazakhstan).

i) Temperature

Temperature recordings from all three stations closest to the 2010/11 event sites show similar patterns, indicating a high probability that they are representative of conditions at the event sites: substantial departures from long-term variation in January and May 2010, and February 2011 (Fig. 7).

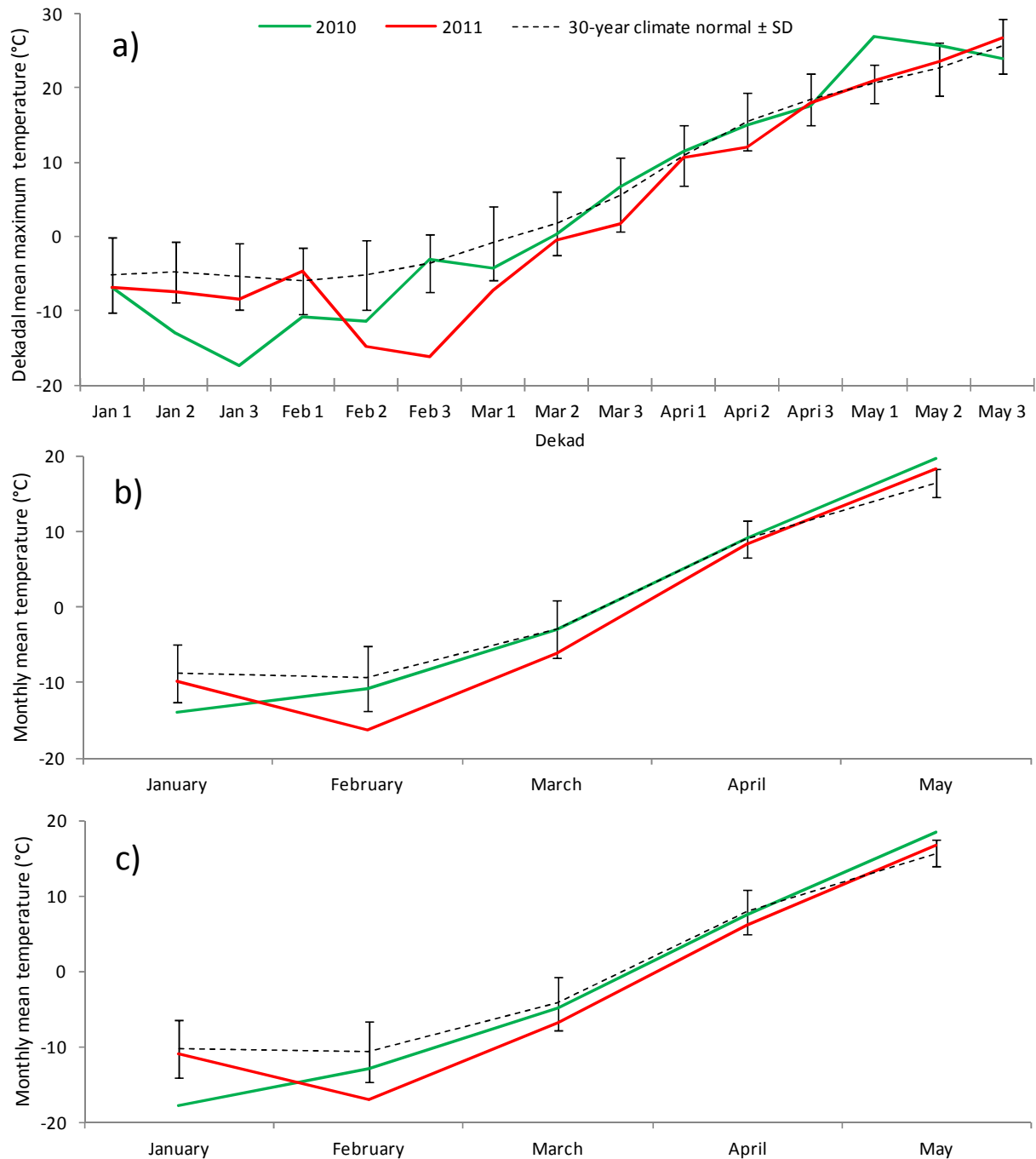


Figure 6. Mean temperatures recorded at Aleksandrov-Gaj, Russia (a; dekadal maximum), and Furmanovo (b; monthly) and Uralsk (c; monthly), Kazakhstan; plotted in order of distance from 2010/11 mortality event sites (80, 155 and 300 km, respectively).

Mean maximum temperatures in Aleksandrov-Gaj, Russia, 80km from the event sites, reached a nadir of $-17.3\text{ }^{\circ}\text{C}$ in late January 2010, almost $12\text{ }^{\circ}\text{C}$ below the 30-year climate normal of $-5.4\text{ }^{\circ}\text{C} \pm 4.5$; and peaked in early May 2010 at $27.0\text{ }^{\circ}\text{C}$, over $6\text{ }^{\circ}\text{C}$ above a normal of $20.7\text{ }^{\circ}\text{C} \pm 2.6$ for the period (Fig. 7a). Winter 2011 was similarly unusually cold at times, reaching a low of $-16.3\text{ }^{\circ}\text{C}$ in late February, almost $13\text{ }^{\circ}\text{C}$ below a normal of $-3.5\text{ }^{\circ}\text{C} \pm 3.9$; but with no corresponding warm spell during or immediately prior to the die-off event.

Without statistical analysis it was not possible to conclusively accept the hypothesis that prior to the events in 2010/11, in the vicinity of the mortality events, temperature departed significantly from long-term variation for that time of year, however results indicate substantial departures took place in both years. The pattern of variation in both years was not concordant however, with regard to high temperatures in May. This is significant as warm temperatures prior to the events were hypothesised to be a potential factor contributing to unusual pastures. It is possible that particularly cold spells in the winter of both years may have been a factor.

Temperature recordings from the three stations closest to the 1988 mortality event epicentre also show broadly similar patterns to each other, indicating a high probability that they are representative of the broad die-off region: below average temperatures in February 1988 and above average in April 1988 (Fig. 8), although not substantially so. Mean maximum temperatures in Turgaj, Kazakhstan, 154 km from the event epicentre, were lowest in early February at $-17.2\text{ }^{\circ}\text{C}$, just over $5\text{ }^{\circ}\text{C}$ below the 30-year climate normal of $-11.9\text{ }^{\circ}\text{C} \pm 4.7$; and peaked in late April at $20.4\text{ }^{\circ}\text{C}$, almost $3\text{ }^{\circ}\text{C}$ above a normal of $17.5\text{ }^{\circ}\text{C} \pm 3.7$ for the period (Fig. 8a). It is highly unlikely however that these derivations are significant. Consequently, it was not possible to accept the hypothesis that variations in temperature found in relation to the 2010/11 mortality events correlated with similar variations surrounding the 1988 event.

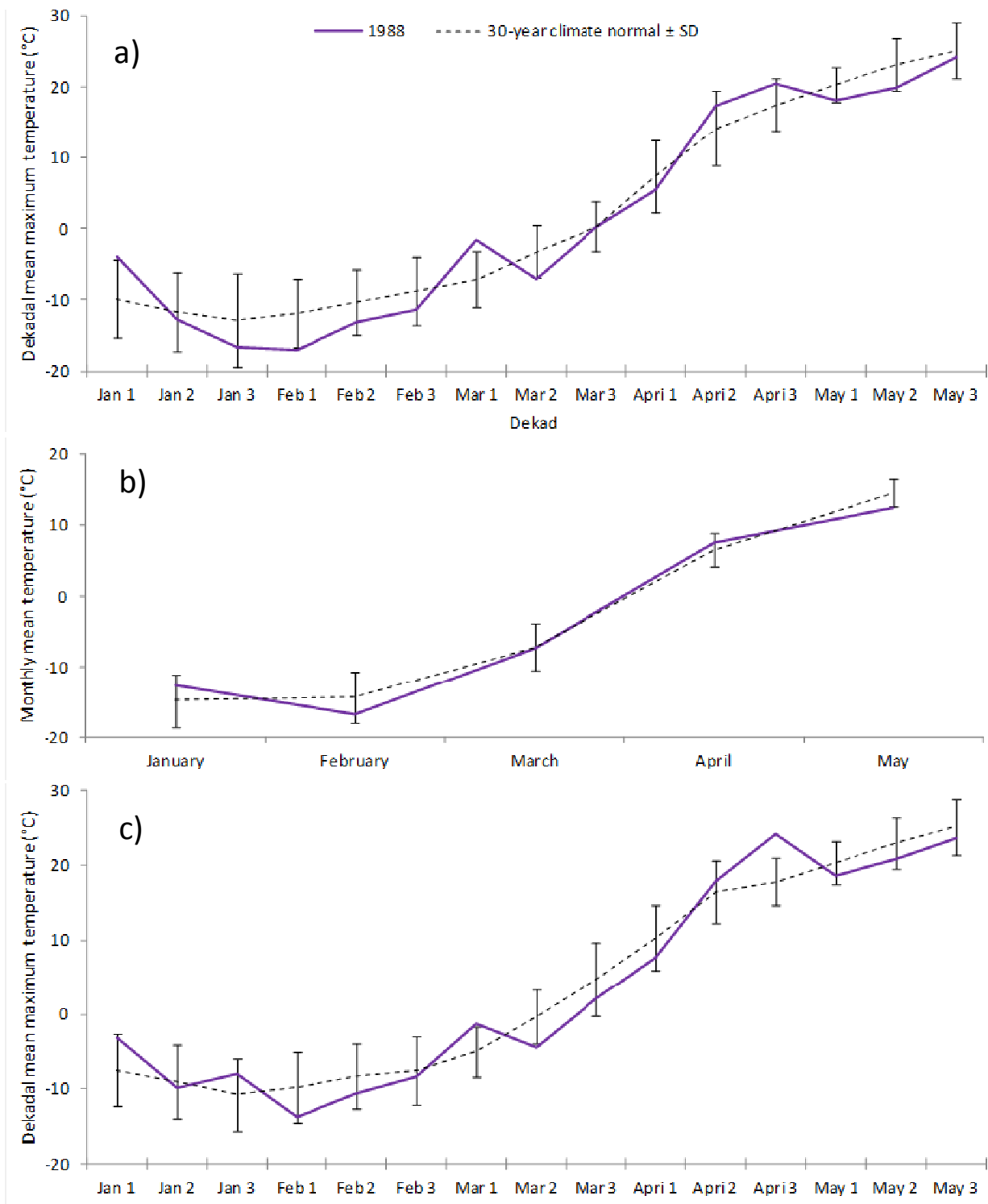


Figure 8. Mean temperatures recorded at Turgaj (a; dekadal maximum), Karsakpaj (b; monthly) and Zhezkazgan (c; dekadal maximum), Kazakhstan; plotted in order of distance from 1988 mortality event epicentre (154, 219 and 232 km, respectively).

ii) Precipitation

Total precipitation recordings from the two stations closest to the 2010/11 mortality event sites showed no similarity in composition, consequently it was unknown if conditions were representative (Fig. 9).

This finding was not remarkable given the large distance between the two stations (80 and 429 km

distant from the event sites), the location of the furthest station, in Astrakhan, Russia, next to the Caspian Sea, which may confer substantially different climatic characteristics, and precipitation's spatially heterogeneous nature in arid ecosystems (Noy-Meier, 1973).

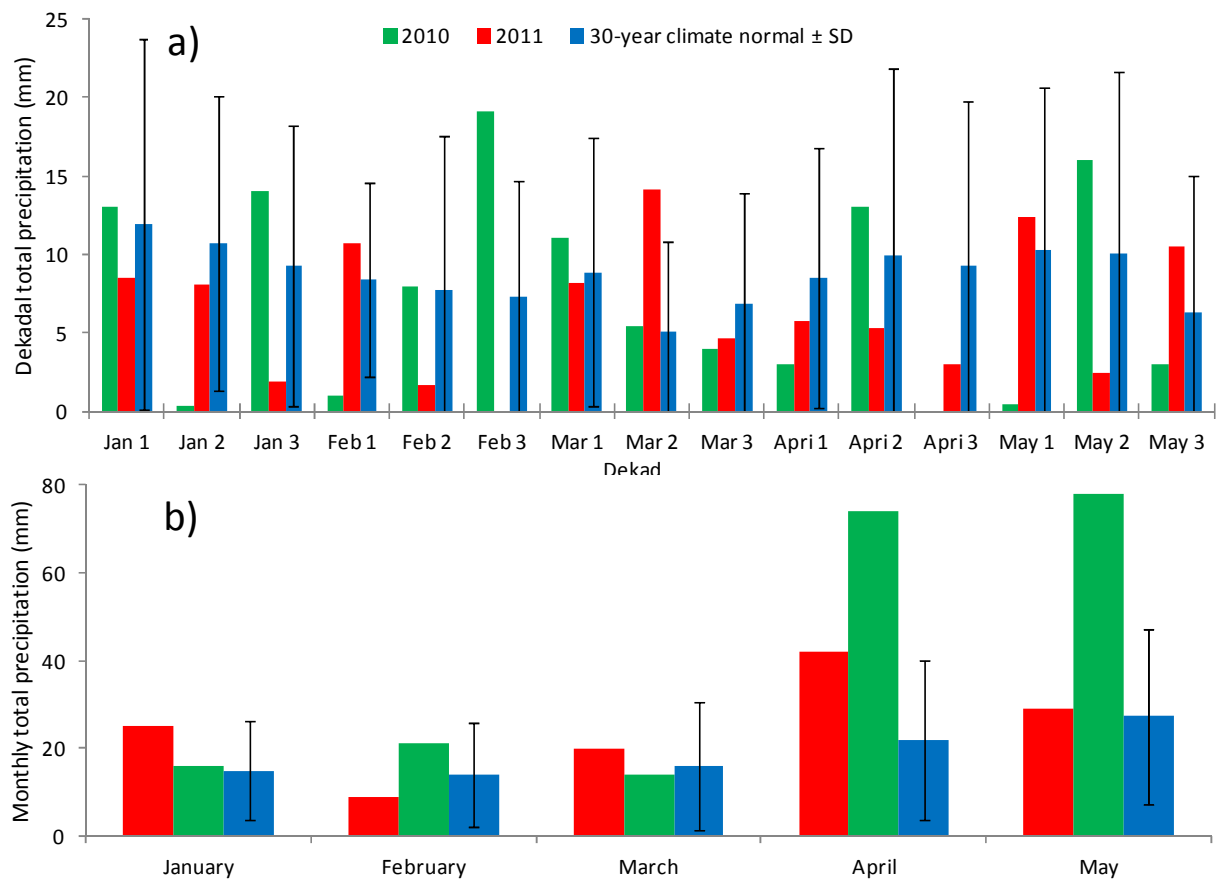


Figure 9. Dekadal and monthly total precipitation recorded at Aleksandrov-Gaj (a) and Astrakhan (b), Russia, respectively; plotted in order of distance from 2010/11 mortality event sites (80 and 429 km, respectively).

Data from the nearest station (Fig. 9a) showed little departure from long-term variation prior to 2010/11 events, with all dekads within the bounds of extremely high variation, except for high levels in late February 2010 and mid March 2011. These peaks were not sustained however with total precipitation in the 3 months prior to the events in 2010 and 2011 of 72 mm and 56 mm, respectively, in comparison to 76 mm mean precipitation over 30 years. Furthermore, immediately prior to the events no one dekad showed substantial departure from normals, which might have explained short-term changes in forage moisture content. Interestingly, 13 mm of the 16mm total precipitation recorded in mid May 2010 fell in 24 hours 5 days prior to the onset of mortalities. A similar pattern was not repeated in 2011, however.

Without further data it was not possible to test the hypothesis that precipitation, in the vicinity of the 2010/11 events, departed significantly from long-term variation, however the little data collected

indicated no noteworthy departure from norms. Whilst this data deficiency precluded the possibility of testing the hypothesis that variations in precipitation found prior to the 2010/11 events correlated with similar variations prior to the 1988 event, it was interesting to note that total precipitation recorded at the three stations closest to the 1988 event epicentre also showed little departure from long-term variation (Fig. 10). Total precipitation levels recorded at the two stations nearest to the event epicentre for January to May 1988 were very low, but not unusually so given the high degree of variation.

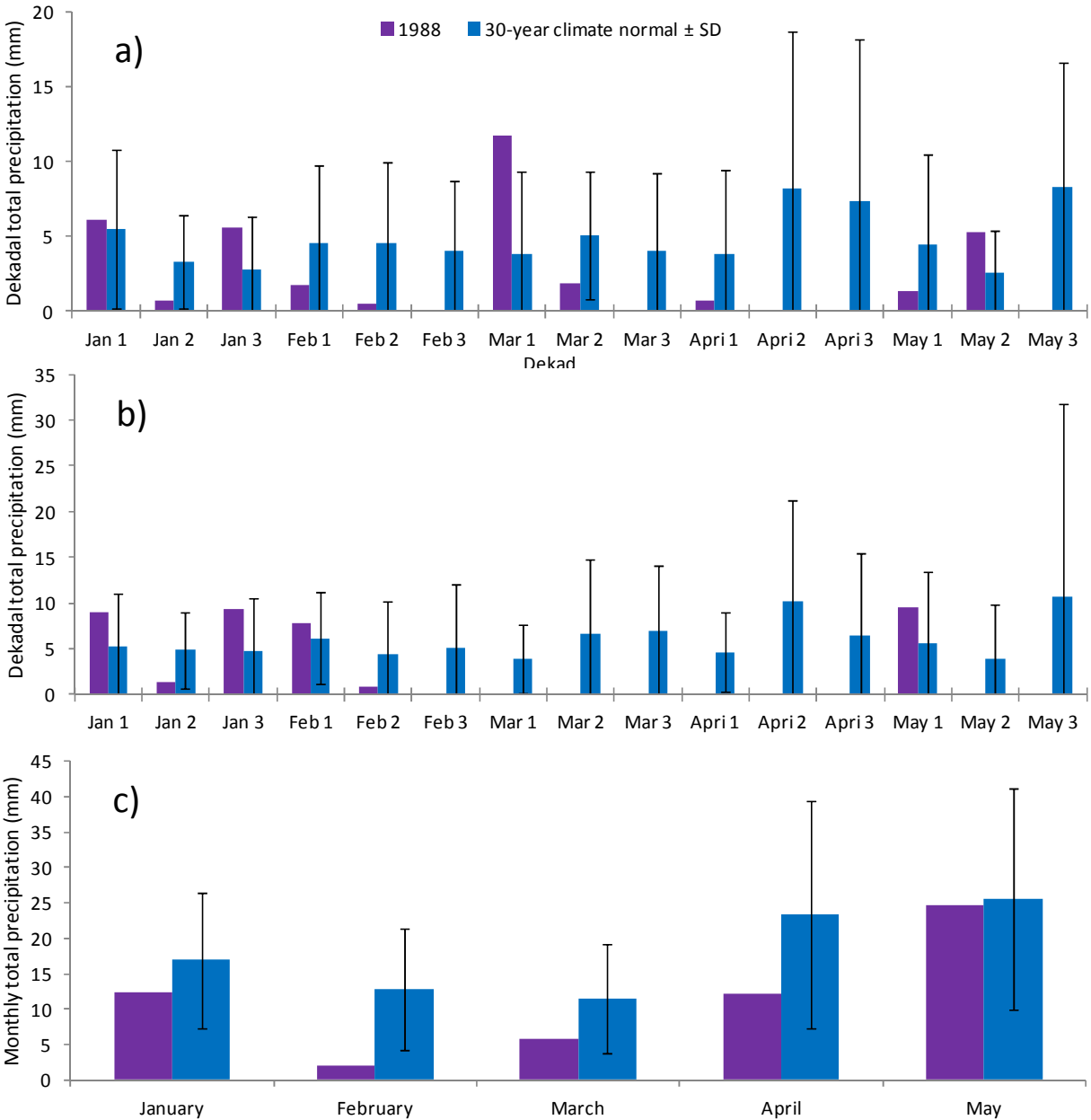


Figure 10. Total precipitation recorded at Turgaj (a; dekadal), Zhezkazgan (b; dekadal) and Kustanay (c; monthly), Kazakhstan; plotted in order of distance from 1988 mortality event epicentre (154, 232 and 420 km, respectively).

(2) Satellite imagery

i) Temporal

Neither mean NDVI (0.583 ± 0.057 ; Fig. 11a) nor mean NDWI (0.267 ± 0.096 ; Fig. 11c) for the period of the die-off in 2010 differed substantially from long-term means (0.579 ± 0.079 and 0.268 ± 0.106 , respectively). Furthermore, mean NDVI (0.528 ± 0.080 ; Fig. 11b) and NDWI (0.178 ± 0.087 ; Fig. 11d) for the period of the die-off in 2011, whilst more divergent from long-term means (0.553 ± 0.073 and 0.245 ± 0.099 , respectively), were both still within one standard deviation. Consequently, it was not possible to accept the hypothesis that plant productivity and/or moisture content in the die-off zones, during the events, departed significantly from long-term variation.

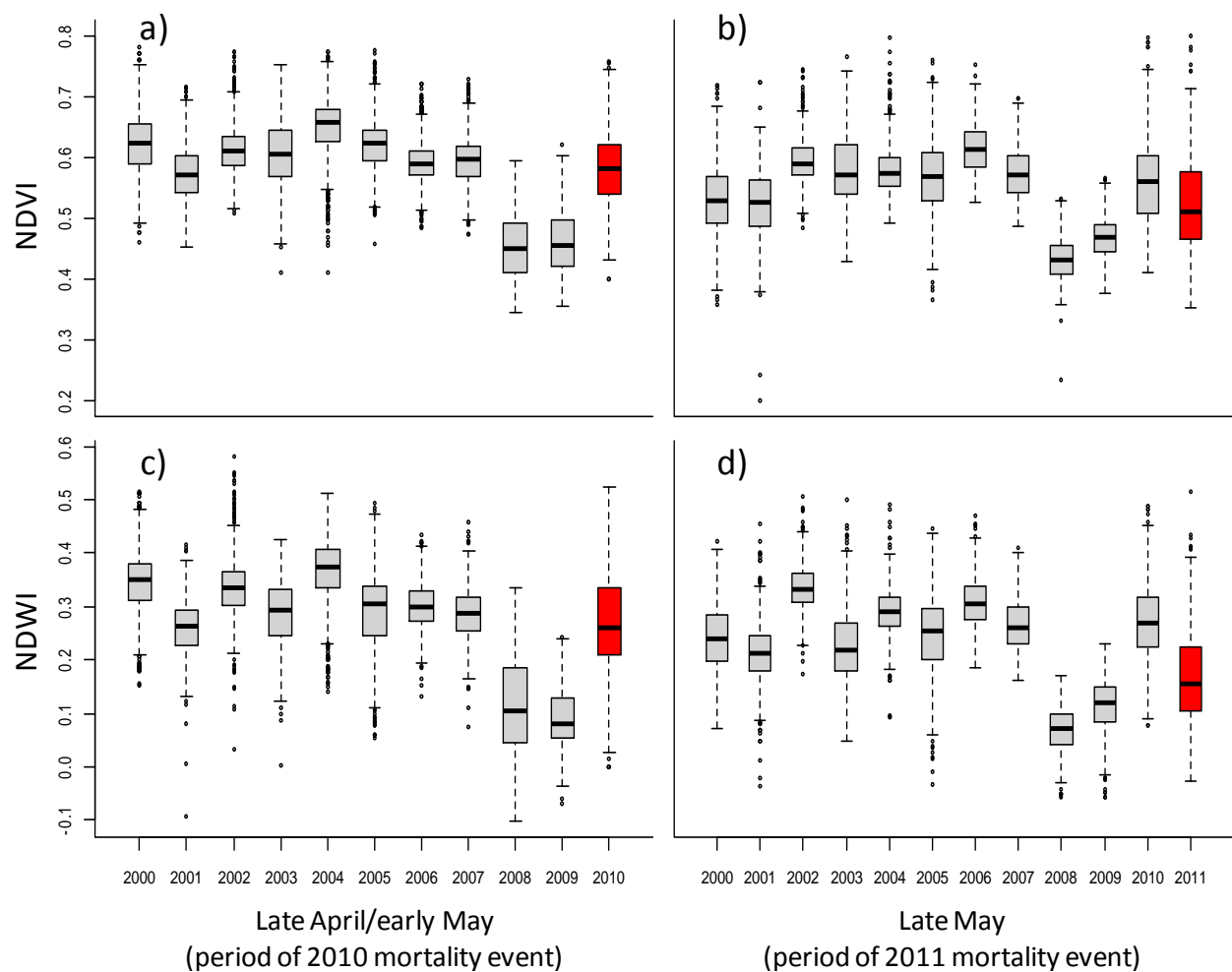


Figure 11. NDVI (a, b) and NDWI (c, d) indices derived from composite 16-day 250m resolution MODIS imagery of die-off zones for late April/early May (corresponding to period of 2010 mortality event; a, c) and late May (corresponding to period of 2011 mortality event; b, d) in comparison to corresponding periods in prior 10 or 11 years, respectively. Event year highlighted in red.

Interestingly, mean NDVI and NDWI in late April/early May 2008 (0.455 ± 0.053 and 0.118 ± 0.088 , respectively) and 2009 (0.460 ± 0.046 and 0.089 ± 0.048 , respectively), and late May in 2008 ($0.438 \pm$

0.034 and 0.074 ± 0.048 , respectively) and 2009 (0.473 ± 0.034 and 0.117 ± 0.058 , respectively), were all well below long-term means. These results indicate substantially reduced plant productivity and moisture content in the two years prior to the events; potentially altering pasture attributes, or indicating environmental conditions which could predicate pasture alteration in subsequent years.

ii) Spatial

Satellite imagery from the period of the die-offs revealed no significant difference in mean NDVI between the die-off zones and their surrounding landscapes in 2010 (0.583 ± 0.094 vs. $0.582 \pm$, respectively; Two sample t-test, $p = 0.874$; Figs. 12a/13a) and 2011 (0.526 ± 0.088 vs. $0.528 \pm$, respectively; Two sample t-test, $p = 0.589$; Fig. 12b/13b). Consequently, it was not possible to accept the hypothesis that plant productivity in the die-off zones, during the events, varied significantly from that of the surrounding landscape.

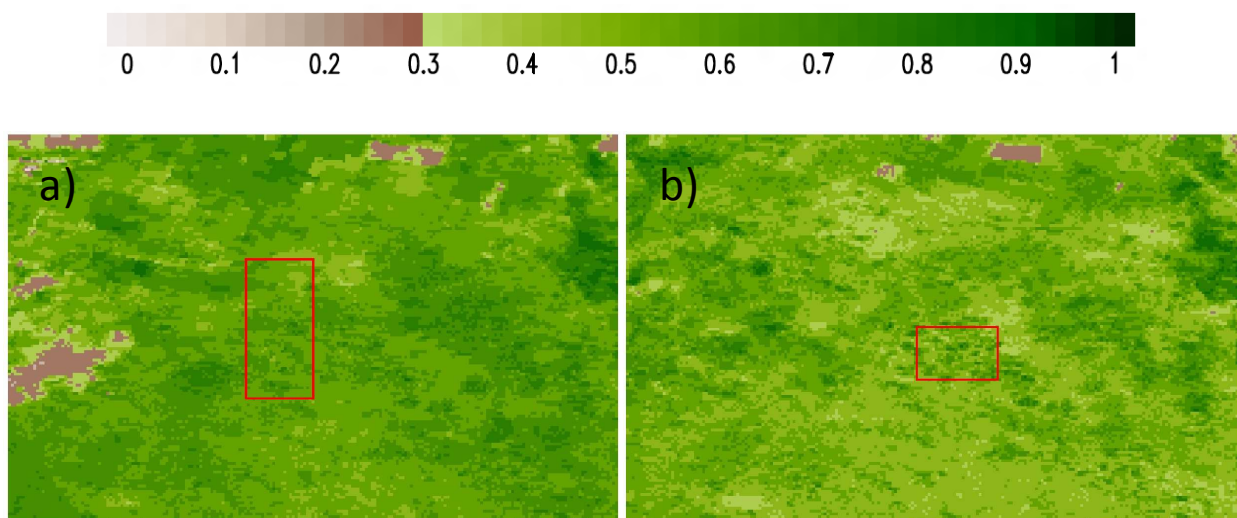


Figure 12. Pseudo-coloured MOD13Q1 16-day 250 m resolution NDVI imagery of 50 x 50 km area surrounding 2010/11 mortality events for period of die-off in 2010 (a) and 2011 (b). Die-off zones bordered in red. Colour palette unit-less ratio of reflectances ranging from -0.2 to 1; higher values indicate higher plant density (as a proxy for productivity).

However, mean NDWI of the die-off zones was significantly *lower* than that of their surrounding landscapes in both 2010 (0.267 ± 0.096 vs. 0.290 ± 0.123 ; $t(1282) = 7.71$, $p = 2.53E-14$; Fig. 13c) and 2011 (0.178 ± 0.087 vs. 0.210 ± 0.124 ; $t(538) = 8.28$, $p = 1.01E-15$; Fig. 13d). Consequently, it was possible to accept the hypothesis that plant moisture content in the die-off zones, during the events, varied significantly from that of the surrounding landscape.

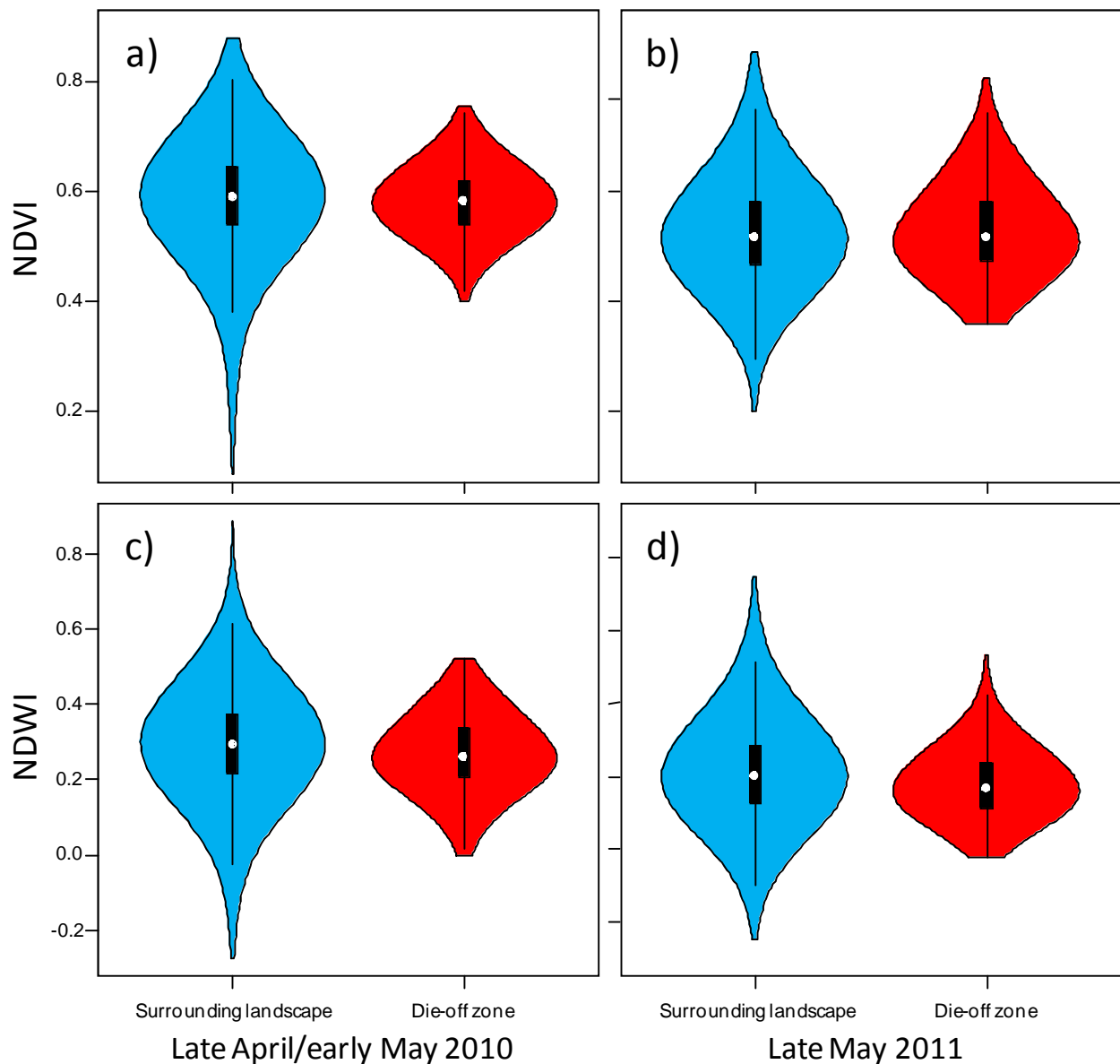


Figure 13. NDVI (a, b) and NDWI (c, d) indices derived from composite 16-day 250m resolution MODIS imagery during mortality events in late April/early May 2010 (a, c) and late May 2011 (b, d). Die-off zones shown in red; 50 x 50 km area surrounding die-off zones shown in blue. No significant difference in mean NDVI between zone and landscape in either 2010 or 2011 (Two sample t-test, $p = 0.874$ and $p = 0.589$, respectively). Significant difference in mean NDWI between zone and landscape in both years (Two sample t-test, $p < 0.05$).

(3) Summary

i) Mortality events in 2010/11

Results indicate substantial, but statistically unverified, departures in temperature from long-term variation prior to the mortality events in 2010/11: particularly cold winters in both years, and warm temperatures in late spring 2010, but not in 2011. Precipitation levels in the same periods however were within normal levels; although these results may not be representative. Plant productivity and moisture content in the die-off zones in both years were consistent with long-term variation. Vegetation moisture

content, but not productivity, was significantly lower in the die-off zones compared with the surrounding landscape at the time of the events.

ii) Correlation with event in 1988

In comparison to the 2010/11 events temperature levels prior to the 1988 event were within normal levels. Insufficient precipitation and location data (for vegetation analysis) limited further comparisons.

IV. Discussion

(1) 2010/11 mortality events

i) Weather

Whilst high temperatures prior to the events have been hypothesised as a potential factor in unusually fast-growing pastures, their absence in 2011 is not unexpected: primary production in semi-arid environments is likely to be *negatively* affected by high temperatures and only when in conjunction with persistent low precipitation resulting in drought (Noy-Meier, 1973). Particularly productive pastures only are associated with ruminal dysfunction (Kahn, 2005). Lower than average winter temperatures could have increased production through the limitation of evaporation, thereby raising soil moisture levels for utilisation in spring; but this is likely to be balanced by the negative effects of an extremely cold winter on plant survival, for example, Wesche *et al.* (2006) found a reduction in the viability of frost-treated seeds of desert steppe species.

High precipitation would have had a profound effect on production, and potentially on plant moisture content, but this was not observed in the limited data available. Precipitation in arid ecosystems is extremely spatially, as well as temporally, heterogeneous; at scales down to 0.1 km (Noy-Meier, 1973). Shepherd and Caughley (1987) have suggested that mean precipitation values in high-variability systems are less informative than variability measures. The large stochastic element in precipitation thus makes determining effects difficult to assess and limits the explanatory power of non-local data. Regardless of data deficiencies, any abnormal patterns would be correlated with similar changes in NDVI as precipitation and productivity are effectively confounded. Observed NDVIs within norms suggest equally typical precipitation levels.

Extreme climatic variation has been implicated in large saiga population fluctuations historically, but with regard to *dzhut* occurrence: deep or thawed and refrozen snow limiting access to forage (Robinson and Milner-Gulland, 2003). Climate warming has also been responsible for vegetation-mediated reduction in the vital rates of other ungulates (Post *et al.*, 2008). Unusual weather variables are unlikely to have been a major factor for the events in question however.

ii) Vegetation

Although observed mean NDVI levels were within long-term variation, and contiguous with the surrounding landscape, they were higher than those recorded by Singh *et al.* (2010a) from images of saiga spring distribution grounds during calving over the last decade; probably due to the calving grounds' abnormally high latitudes in 2010/11. Calving purposefully coincides with rapid grass growth (Bekenov *et al.* 1998), most likely to satisfy the demands of lactation, but this can be a high-risk strategy,

for example, fast-growing pastures have been associated with ruminal dysfunction in cattle (Kahn, 2005). However, as saigas in the surrounding landscape were unaffected, it is unlikely that productivity is a factor.

Of more relevance is the significant difference in NDWI between die-off zones and the surrounding landscape; although crucially mean NDWI was lower in die-off zones and did not depart from long-term variation. This finding directly contradicts the hypothesis that high plant moisture content was an important attribute in ruminal dysfunction, but indicates a potential difference in the soil or vegetation of die-off zones, lending credence to the hypothesis that events were location-, but not weather- or time-, dependent. NDWI has previously been used to reveal differences in plant composition (Xiao *et al.*, 2002), and lower soil moisture, which is also reflected in NDWI, is an indicator of a lower concentration of perennials (Ludwig *et al.* 2005), indicating that species composition may be an important factor. Forage moisture content is also not associated with ruminal dysfunction in the literature, supporting my findings. Moisture can be associated through the presence of dew (Majak *et al.*, 1995) which by virtue of its transience would not be identified by imagery. Dew is formed when appropriate levels of air humidity and ground/near surface air temperature combine; generally early mornings after cloudless nights (Agam & Berliner, 2006). Data for these variables were not obtained in this study.

iii) Ruminal dysfunction

The veterinary literature makes a distinction between AIP and a similar affliction of livestock called bloat (Fig. 14).



Figure 14. Post-mortem of cow suffering from feed-associated bloat, demonstrating high pressures developed in rumen (Cheng *et al.*, 1998); in contrast to AIP in which symptoms are associated with lung toxicosis.

AIP generally occurs late in the growing season (~ September, Northern Hemisphere) when livestock are moved abruptly onto fast-growing, L-tryptophan-rich pastures. Acute respiratory distress develops in response to metabolic toxins. Symptom onset is normally 5 to 10 days and morbidity rates can be >50%

(Kahn, 2005). The condition has been observed in wild ruminants, including nyala (*Nyala angasii*) and grey duikers (*Sylvicapra grimmia*) (Lane, 2012).

Conversely, bloat occurs early in the growing season (~ May) and can result in sudden death from the build-up of ruminal gases, with mortality rates of >20%. High-protein, legume-rich forage, particularly alfalfa (*Medicago sativa*) and clovers (*Trifolium spp.*) in early growth stage (Majak *et al.* 1995) trigger symptoms which develop over 2 to 3 days (Kahn, 2005). Dew exacerbates the condition: livestock feeding in early daylight hours had increased susceptibility (Majak *et al.* 1995). Lactation increases its severity in sheep (Colvin & Backus, 1988). Bloat occurrence is also not associated with variation in weather (Majak *et al.* 1995).

Three factors preferentially indicate a condition similar to bloat: firstly, die-offs occurred early in the growing season; secondly, lower recorded mean NDWI in die-off zones, as dry grasses hold less L-tryptophan (Haskell, 2009); lastly, contiguous die-off zone/broader landscape NDVI, as AIP is generally associated with abrupt change in forage quality. However, Wobeser (2007) highlights the risks of extrapolating disease determinants in livestock to wild animals as susceptibility and response varies substantially between species.

iv) Implications

This research project aimed to explore assumptions underlying the current hypothesis. My findings, in combination with a literature review, suggest a revision (Fig. 15): a combination of topography, namely depressions which encourage bloat-forming plants, and improvement by farmers for hay-making, led to legume-rich pasture formation. If saigas were grazing in early daylight hours, as is often observed (Bekenov *et al.*, 1998), and conditions were suitable, the disorder may have been exacerbated by dew.

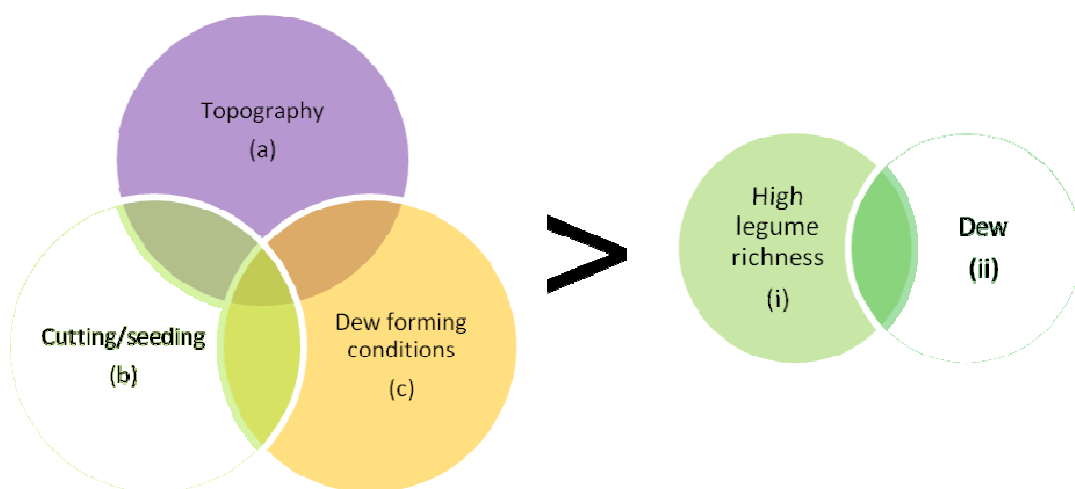


Figure 15. Revised hypothesis for saiga mass mortality events in 2010/11. Results indicate combination of unusual topography (a), cutting/seeding (b) and conditions necessary for dew formation (d) are factors in the development of legume-rich pastures (i), potentially with some quantity of dew (ii).

These findings have implications for the likelihood of future events and management strategies. Given the events' location-dependent nature the recent die-off zone is an ongoing risk. Human disturbance and changing climate have driven and will drive changes in calving areas, further north and away from settlements (Singh *et al.*, 2010a). Pastures with similar attributes in the saiga's future range thus pose a potential hazard and must be defined along with methods for discouraging saiga. Wang *et al.* (2012) emphasize that bloat's unpredictability and complex aetiology making prevention difficult, but the most common method is alfalfa-rich pasture avoidance. Majak *et al.* (1995) also found increased bloat occurrence in cattle if grazing was disturbed, even after symptom onset, as continued feeding encourages forage movement through the gut. Therefore if saigas are found to have been feeding in alfalfa-rich zones for several hours it may be more harmful to disturb them than to wait until grazing finishes.

(2) Other mortality events

Data deficiencies precluded more detailed analysis of the 1988 event. As results indicate that the 2010/11 events are not weather related it is possible that the 1988 event is also pasture associated, however circumstances surrounding the latter vary considerably: mortalities were observed in locations across central Kazakhstan, and in the same area as livestock, which were unaffected (Turgai Regional Executive Committee, 1988). Notably, adult saigas were observed in poor, undernourished condition.

High mortality levels, of biotic and abiotic origin, have been recorded during saiga spring calving throughout the past century. In addition to pasteurellosis-ascribed events during the 1980s, 6 foot-and-mouth epidemics were documented between 1955 and 1974; in 1967 alone resulting in ~50,000 calf deaths (Bekenov *et al.* 1998). These, the events of 2010/11, and an unidentified but potentially novel syndrome recorded in May 2012 (RFE/RL, 2012), indicate that saigas are highly susceptible to natural die-offs in spring. Calving is timed and located to coincide with high plant productivity and minimal disturbance (Singh *et al.* 2010a); in dense concentrations of > 600 animals/km² (Bekenov *et al.*, 1998). Whilst aggregations reduce predation risk they are a high-risk strategy with regard to both infectious disease transmission and non-infectious disease susceptibility (Wobeser, 2007). The timing soon after winter may render adult saigas more susceptible to disease and abiotic factors if weakened by extreme conditions (Lundervold, 2001); in addition to the stress of parturition. Calves are also at greater risk of climatic extremes, including drought (Fadeev & Sludskii, 1982) and frosts or cold rain (Bekenov *et al.*, 1998).

Whilst addressing risk of specific syndromes is important it is more urgent to address the greater risk of *any* natural mortality at a time of when saigas appear to be particularly vulnerable, through the optimisation of factors driving calving site selection: decreasing disturbance from human activities and,

potentially, supplemental feeding in years with low pasture growth. Saiga mass mortalities appear to be a natural occurrence, presumably balanced historically by large population sizes, providing an argument for conservation activities which promote an increase in population size from current low levels.

(3) Caveats

The most significant factor that methods utilised in this study cannot address is the scale at which hypothesised factors are acting. Precipitation varies over small distances and microclimatic variables not measured here may be influencing dew formation. More importantly, species composition and productivity may be influenced by topography and pasture improvement at scales finer than the imagery employed and the area assessed. The literature indicated a broad die-off zone measured in km² but patches within this landscape of >100 m² may be more relevant (see Fig. 16 for indication of vegetation patchiness in die-off zones). Moreover, saigas may be moving among patches between grazing and symptom onset, hampering analysis. Satellite imagery may be useful if scale and patch attributes are first sampled locally for plant composition before implementation of a region-wide analysis employing fine-scale imagery-based vegetation mapping, e.g. Landsat 7 imagery (15 m resolution; Markham *et al.*, 2010).



Figure 16. Aerial picture of die-off zone during mortality event in 2010 illustrating patchiness of vegetation. Fine white points are saiga carcasses, indicating scale of patches (Kock *et al.*, 2012).

There are also specific issues with using vegetation indices as proxies for plant attributes. NDVI and NDWI can be adversely affected by albedo and topography (Chen *et al.*, 1998). NDWI is susceptible to soil background effects (Wang *et al.* 2008); considerable in sparse semiarid environments. Furthermore, without statistical analysis all inferences cannot be considered conclusive. More importantly, this

analysis only explored assumptions underlying the current hypothesis. Unconsidered factors may also be involved, for example, soil type.

(4) Conclusion

This study has helped to clarify circumstances surrounding mass mortalities of a critically endangered species, which may have been precipitated indirectly by human activities: via alteration of its environment through farming practices, and its distribution through disturbance and climate change. Similar examples are reported with increasing frequency, for example chytrid fungus die-offs in amphibians which are exacerbated by climate change and pollution (Pound *et al.*, 2006). Despite projections that such events will become more common they have yet to be properly characterised or their significance for conservation fully comprehended (Ameca y Juarez, 2012). The elucidation of events such as that reported by this study will hopefully bring greater attention to this pressing issue.

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