Effect of terrain heterogeneity on feeding site selection and livestock movement patterns

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Livestock movements associated with feeding site selection play a major role in grazing distribution and they can affect the forage available for diet selection. This study evaluated day-to-day movement patterns of cattle in pastures with gentle topography and in pastures with rugged and diverse terrain. Cows regularly alternated among sites in homogeneous pastures with gentle topography and stayed longer in sites within diverse pastures with rough terrain, which likely helped the cattle mix their diets.

Effect of terrain heterogeneity on feeding site selection and livestock movement patterns

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Abstract. Feeding site selection is a critical part of livestock foraging that can constrain and/or increase the choices available during diet selection. When livestock choose new feeding sites vegetation and nutrient profiles can differ from other areas, especially in heterogeneous environments with rugged terrain. Correspondingly, livestock should remain longer in feeding sites in rugged heterogeneous pastures than in homogeneous pastures where animals may alternate among feeding sites to facilitate diet mixing and to prevent satiation. The objective of this study was evaluate how terrain and corresponding heterogeneity may affect the sequence and pattern of feeding site selection of free-roaming livestock. Grazing patterns of mature cows were evaluated on 6 ranches located in Arizona, Montana and New Mexico. Eleven to 19 cows were tracked for one to three month periods at each ranch using global positioning system (GPS) collars. Positions were recorded at 10 or 15 minute intervals and used to identify where cows grazed during the early morning (0500 to 1000 hours). Pastures (336 to 9740 ha) at each ranch were divided into 7 to 9 sections (48 to 1082 ha) as an indicator of feeding sites. Classification was based on cattle density and topographical and vegetation types. Sequences of daily section selection were evaluated using transition matrixes. For all ranches, the sequence of section selection differed from what would be expected by chance indicating that the section selected on the following day depended on the section selected on the previous day. For ranches with relatively gentle terrain, cattle selected different feeding sites about 70% of the tracking period. In contrast, cows at the ranch with the largest pasture and enclosing both mountainous and gentle terrain cows stayed in the same feeding site for over ten successive days for 42% of the tracking period. Smaller pastures with only mountainous terrain were intermediate. Cows grazing gentle topography and relatively homogeneous vegetation

alternate among feeding sites (sections in this study) more frequently than cows grazing pastures with more rugged topography and more heterogeneous vegetation. This pattern could help livestock mix forages and select a more diverse diet.

Additional key words: distribution, cattle, grazing behaviour, GPS tracking,

Introduction

Livestock grazing behaviour is rich in complexity, because processes occur at multiple spatial and temporal scales (Senft *et al.* 1987). At finer scales, diet and patch selection, forage nutritive levels, presence of secondary compounds, and forage quantity are critical criteria used by livestock during selection (Bailey *et al.* 1996). At coarser scales (e.g., feeding site selection), abiotic factors such as slope and horizontal and vertical distance to water affect foraging behaviour and can modify decision processes that occur at finer scales such as diet selection (Bailey 2005). Livestock typically avoid areas far from water (Valentine 1947) and steep slopes (Mueggler 1965). Because foraging is a hierarchical process (Senft *et al.* 1987), choices made at coarser scales can constrain alternatives available at finer scales. When livestock select a feeding site (Bailey *et al.* 1996), the forages from which they can select are limited to those that are available in that area.

Feeding site selection can be modified more readily by managers than diet selection (Bailey 2005). In diet selection, animals make decisions every time they bite, once every one to three seconds. Livestock choose among a multitude of plant species on rangelands, but they usually focus on few species during a grazing bout. For example, 3 or 4 species made up the majority of the diet, but cattle consumed over 25 different species on Chihuahuan Desert rangeland (Rosiere *et al.* 1975). Correspondingly, it is difficult to apply diet training to livestock on rangelands and most diet training is done in pens or small pastures where diet selection can be constrained. Consequently, researchers have used early learning to increase use of a target plants species (Walker *et al.* 1992) and aversion learning to avoid grazing poisonous plants (Ralphs 1992). In contrast, livestock readily respond to management that modifies movement patterns (e.g., herding, development of new water sources, and strategic supplement placement), and these practices can be applied while grazing rangelands.

Bailey and Provenza (2008) suggested that feeding site selection patterns of free-ranging livestock are influenced by both the availability of preferred forages and satiation. Optimal foraging theory predicts that herbivores should switch between feeding sites as forage is depleted and nutrient intake rate becomes noticeably less than levels that can be obtained other areas of the habitat (Charnov 1976). The mechanism that large herbivores likely use to implement this strategy is through 'giving up rules' (McNair 1982; Stephens and Krebs 1986). However, livestock often move between feeding sites before changes in forage availability would likely be noticed. Bailey *et al.* (1990) found that cattle rarely stayed in the same location for more than two consecutive days in a row in a relatively homogenous pasture in Colorado. In an Oklahoma study, steers alternated among homogenous patches, and selected a nutrient rich patch for several consecutive days in a heterogeneous pasture (Bailey 1995).

The satiety hypothesis (Provenza 1996) was suggested by Bailey and Provenza (2008) as a possible explanation for the tendency of livestock to move among feeding sites. Livestock may become satiated because of the presence of toxins or nutrient imbalances resulting from excessive amounts of certain types of forages. For example, livestock that consume large quantities of forage that are high in protein are more likely to seek out foods that are higher in energy with lower protein content (Villalba and Provenza 1999). Livestock will become satiated if they consume excessive quantities of secondary compounds because of post-ingestive feedback (Launchbaugh *et al.* 1993; Burritt and Provenza 2000; Launchbaugh and Howery 2005). Mixing different forages can also reduce the impacts of secondary compounds. Lyman *et al.* (2008) found that sheep intake was greater when the diet contained a mix of forages with differing secondary compound than when the forages were fed individually. The sequence that forages containing secondary compounds are consumed can affect impacts of post-ingestive feedback and corresponding changes in intake (Lyman *et al.* 2011). Because feeding sites usually differ in botanical composition and/or quantity and quality of forages, moving from one feeding site to another has the potential to increase diversity of the diet by providing opportunities for diet mixing. Villalba *et al.* (2011) found that sheep fed secondary compounds moved to sections of a pasture that contained forages that would reduce the negative impacts of the secondary compounds. French shepherds move their flocks from one area to another to stimulate appetite and increase intake by forcing sheep to mix their diets and increase overall diet diversity (Meuret *et al.* 1994; Provenza and Papachristou 2009; Meuret and Provenza 2014a, 2014b).

Free-roaming livestock may move among feeding sites to facilitate diet mixing and to avoid becoming satiated at any given site. Bailey and Provenza (2008) suggest that staying in one spatial location can be aversive resulting in animal becoming satiated with feeding site.

Stereotypic behaviour displayed by zoo animals (Bashaw *et al.* 2001) and livestock kept in small pens (Redbo 1990) suggest that animals may become satiated with a spatial location. Restricting the area that livestock and other animals can move increases stress (Morgan and Tromborg 2007). In addition to impacts of post-ingestive feedback, livestock may become satiated with a feeding site and become motivated to move to other sites because of environmental or other behavioural factors. The pattern of feeding site selection of livestock may vary based on the heterogeneity found within the pasture. If feeding sites are homogeneous, livestock may readily switch among sites because animals may perceive that they have limited opportunity to mix foods within a given feeding site, and defoliation in the site more readily changes relative levels of resources compared to other sites in homogeneous pastures (Bailey and Provenza 2008). In contrast, cattle can more easily switch between patches in an attempt mix various forages within a feeding site if it is heterogeneous. In rugged topography, feeding sites often contain a variety of forages because of elevation gradients and differences in aspect or soils within the feeding site. Changes in environmental conditions and ecological processes along elevation gradients results in plant species diversity (Lomolino 2001), especially in desert regions (Whittaker and Niering 1975). Differences in forage diversity between gentle terrain and rugged topography may be exasperated by historic cattle grazing patterns. In gentle terrain, cattle readily travel the entire pasture consuming preferred plants, which may reduce their abundance if stocking levels are high (Bailey 2005). In contrast, cattle graze often graze unevenly in rugged terrain by avoiding steep slopes (Mueggler 1965) and high elevations (Roath and Krueger 1982) resulting in greater vegetative diversity between steep and more gentle areas. Correspondingly, livestock should remain in feeding sites in mountainous terrain that usually contain diverse vegetation, and switch to another feeding site less frequently than in homogeneous pastures composed of gentle terrain. The objective of this study was to evaluate how terrain and corresponding heterogeneity can affect the sequence and pattern of feeding site selection of free-roaming livestock. We assume that livestock spatial movements among feeding sites is based on the need to mix diets, avoid adverse environmental conditions and perhaps provide environmental enrichment. Cattle apparently have no innate tendency to return to the same place to forage or to regularly move to another location to forage based on maze studies (Hosoi *et al.* 1995). Instead, cattle learned to use the best strategy to avoid 'losing' situations in the maze. We examine day-to-day movement patterns of cattle tracked in extensive pastures in a variety of landscapes to see how this information supports or refutes proposed mechanisms to explain livestock distribution patterns (Bailey *et al.* 1996; Bailey 2005; Launchbaugh and Howery 2005; Bailey and Provenza 2008)

Methods

All procedures used in this study were approved by the New Mexico State University Institutional Animal Care and Use Committee (protocol 2009-10).

Study sites

We used GPS tracking data from six ranches that were collected as part of another study. These ranches are located in differing topography and vegetation types. The Carter Ranch, NMSU College Ranch and NMSU Corona Ranch are located in relatively gentle terrain. The Evans and MSU Thackerary Ranch are located in mountainous terrain. The Todd Ranch is the largest of the study sites and is the most diverse with both mountainous and rugged terrain and large areas of gentle plains (Table 1).

The Carter Ranch is located 25 km north of San Simon, Arizona. Terrain is gentle with some slopes. Dominant grasses are tobosa (*Pleuraphis mutica* Buckley), dropseeds (*Sporobolus* spp.), and grama grasses (*Bouteloua* spp). Dominant shrubs included honey mesquite (*Prosopis glandulosa* Torr.), cresosote [*Larrea tridentata* (DC.) Coville], catclaw acacia (*Acacia greggii* A. Grayand) and whitethorn acacia (*Acacia constricta* Benth).

The Chihuahuan Desert Rangeland Research Center (College Ranch) is managed by New Mexico State University and is located approximately 37 km north of Las Cruces, New Mexico. The terrain is rolling and interspersed with dry watercourses (arroyos) and small ridges. Common grasses included dropseeds,threeawn (*Aristida* spp.) and bush muhly (*Muhlenbergia porteri* Scribn. ex Beal). Dominant shrubs are honey mesquite and creosote.

The Corona Range and Livestock Research Center (Corona Ranch), managed by New Mexico State University, is located 13 km east of Corona, New Mexico. Terrain is rolling with undulating plains. Dominant grasses are blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], New Mexico feathergrass [*Hesperostipa neomexicana* (Thurb. ex J.M. Coult.)

Barkworth] and other grama grasses. Tree cholla [*Cylindropuntia imbricata* (Haw.) F.M. Knuth], is an abundant shrub, and there are scattered juniper trees (*Juniperus* ssp.).

The Evans Ranch is located 57 km southwest of Silver City, NM. Terrain is mountainous with bottom areas containing gentle to moderate slopes. Side oats grama [*Bouteloua curtipendula* (Michx.) Torr.] is the dominant grass, but other grama grasses and tobosa are common. Juniper, live oak (*Quercus* spp.) and mountain mahogany (*Cercocarpus* spp.) are dominant woody species.

The Thackeray Ranch is managed by Montana State University and is located in the Bear's Paw Mountains approximately 25 km south of Havre, Montana. Terrain is mountainous with steep slopes dividing ridges and narrow bottom areas. Dominant grasses at the site are Kentucky bluegrass (*Poa pratensis* L.), rough fescue (*Festuca campestris* Rydb.), bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Á. Löve], and Idaho fescue (*Festuca idahoensis* Elmer). Less than 15% of the pasture contains trees such as ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson) and aspen (*Populus tremuloides* Michx.).

The Todd Ranch is located 11 km northwest of Willcox, Arizona. Terrain is variable with over 50% of the pasture containing mountainous terrain and the remaining area containing bottom lands with gentle slopes. Dominant grasses are dropseeds and sacaton (*Sporobolus* spp.), grama grasses, threeawn (*Aristida* spp.), and tobosa. Common trees and shrubs include mesquite (*Prosopis* spp.), desert willow (*Chilopsis linearis* (Cav.) Sw`eet), acacia (*Acacia* spp.), juniper and oak.

Cattle tracking

Most of the cattle that were tracked with GPS collars were randomly selected from the cows that were scheduled to graze in the study pastures. During 2010 and at the Corona Ranch and Todd Ranch, visual observations collected prior to collaring were used to select cows that were found at the highest elevations, steepest slopes and areas further from water (hill climbers) and cows that were observed at lowest elevations, more gentle slopes and areas closest to water (bottom dwellers). The extreme hill climbers and bottom dwellers classified using these limited visual observations (3 to 7 days of observation) were collared at the Todd Ranch and at the Corona Ranch in 2011. However, Lunt (2013) found that the visual observations used to select cows at the Corona and Todd Ranch were not consistent predictors of the terrain use recorded by GPS tracking data. Correspondingly, we do not know if we picked extreme animals to collar at the Todd Ranch and Corona Ranch in 2011, and the collared animals may be less of a biased sample. The cows tracked at the Thackeray Ranch were developed as part of another study (Bailey *et al.* 2010) and were all sired by the same bull (half sibs).

Cows were tracked with Lotek GPS 3300 global positioning system (GPS) collars. Cows at the Carter and Todd ranch were tracked at 15 minute intervals for two to three months (Table 2), while cows at the CDRRC, Evans Ranch and Thackeray Ranch were tracked at ten minute intervals for one to two months. At the Corona Ranch, cows were tracked at ten minute intervals in 2010 and 2011, and 2012. Cows had calves during the tracking period at the CDRRC, CRLRC, Evans Ranch and Thackeray Ranch. Cows at the Carter and Todd ranch were tracked in the autumn and winter after their calves were weaned, and the cows were not lactating.

Subdivision of pastures into sections

Pastures were subdivided into 6 to 9 sections in an effort to estimate the locations of feeding sites (Table 2). All GPS tracking data from cows in a pasture were used to classify subdivided sections by identifying areas with higher concentrations of cattle through the use of the kernel density function of ArcMap 9.3 (ESRI, Redlands, CA). Digital elevation models, distance from water and vegetation type were also used to classify sections. Areas where cattle were concentrated with similar topography and/or vegetation were included as a section. Contiguous concentrations of cattle that were far from water were separated from areas closer to water. The mean size of these sections varied from 48 to 1082 ha. The variability in size of sections corresponds to the pasture size (Table 2) and the need to limit the number of section to less than ten per pasture to facilitate statistical analyses and better represent the concepts associated with feeding site (Bailey *et al.* 1996; Bailey and Provenza 2008). Examples of the locations of sections and corresponding tracking data are shown for the Carter and Todd Ranches in Figures 1 and 2, respectively.

Sections at the Todd Ranch were 2 to 20 times larger than sections at the other ranches (Table 2). Two sections (1 and 2) at the Todd Ranch were subdivided into 5 subsections that using criteria similar to those described above for selecting sections. A large proportion of section 1 was mountainous terrain, and section 3 was the only section containing primarily gentle terrain (Figure 2). At least 3 tracked cattle used each of the sections for most of the tracking period. The purpose for subdividing these sections was to provide examples of movements within the large sections at the Todd Ranch.

Patterns of pasture use

For all analyses, only tracking data recorded from 0500 to 1000 was used for evaluating the daily selection patterns of the sections. Early morning is usually one of the primary grazing periods (Gregorini 2012), and cow locations during the early morning is a good predictor of where cows were grazing during the previous evening grazing bout (Low *et al.* 1981; Bailey *et al.* 2004). Correspondingly, we determined which section that cows were located each morning during the tracking deployment. If a cow was located in more than one section, the section with the majority of fixes for that morning was considered as the section selected by that cow for analyses of section (feeding site) selection sequences.

The sequence of the section selection was calculated for each collared cow during the deployment, and the data were analysed using first order Markov chains (Bailey *et al.* 1990; Lehner 1996). The dyads of the preceding and following sections selected were evaluated using a transition matrix. Markov chains can be used to evaluate sequences of behaviours by determining if the transitions between behaviours are dependent on each other at a level greater than chance (Lehner 1996). The transition matrix is compared to a random model using Chi-square analyses. If the null hypothesis is rejected, the selection of a section is dependent on the section that was selected the day before. Matrix cells with large Chi-square values indicate large deviations from the random model and can be used to identify transition that occur more or less frequently than expected by chance. Similar to Bailey *et al.* (1990) we used these transition matrixes as a descriptive tool because data from multiple cows were pooled in the matrix and the assumption of stationarity may have been violated (Lehner 1996). However, Markov chain analyses can provide a reasonable framework for evaluating the sequence of selected grazing locations (sections for this analysis).

Transition matrices were used to examine day-to-day changes in where cattle grazed. Cattle usually went to water daily and often left the section (feeding site) to a common water location. There was only one water source at the College Ranch and Corona Ranch, and cattle had to leave the section they were grazing and walk to a water tank at the edge of the pasture to drink. Similarly, cattle left the section at midday and walked to one of the three water locations at the Evans Ranch and Thackeray Ranch The Carter and Todd Ranches had 6 and 20 water sources, respectively. Sections at the Carter and Todd Ranches contained water sources, and cattle did not need to leave a section to water. However, cattle at all ranches could potentially travel from one section to another during the 18 hour interim between morning grazing periods. Even at the Todd Ranch, the maximum distance between sections was less than10 km. The transition matrix analyses allowed us to determine if cows returned to the same section or moved to another section more than what would be expected by chance.

Sequences of daily section selection from all cows at each ranch were entered into different transition matrices. At the Corona Ranch, all cows tracked during each year were entered into separate transition matrices, and separate analyses were completed for 2010, 2011 and 2012.

For sections, 1 and 3 of the Todd Ranch transition matrices (one per section) were used to evaluate day-to-day movements within the same section. Rather than movements from section to section, the transition matrix evaluated the day-to-day movements among sub-sections of a section. Separate transition matrices were used for section 1 and 3 of the Todd Ranch. Only periods, where cows remained continuously in that section were included in the analyses.

In addition, we calculated the number of times that cows returned to the same section of the study pasture on consecutive days. Linear regression was used to evaluate relationship between the size of sections (i.e., pasture size) and the frequency that cows returned to the same section.

Results

Day-to-day movement patterns of at least 13 cows were successfully monitored for over a month each year at the Corona Ranch (Table 2), which represents over 11,000 positions (during the early morning period) and at least 416 dyads (preceding and following sections) per year. Eleven cows at the Carter Ranch and 15 cows at the Todd Ranch were tracked for two to three months, which represented over 15,500 and 21,000 positions (during the early morning period) and 990 and 1350 dyads (preceding and following sections). Similarly, patterns of section selection were based on over one month of tracking on at least 16 cows at the other ranches, which represents over 15,000 positions and at least 608 dyads at each ranch.

For all six ranches, the Chi-square test indicated that section selected (following morning) was dependent ($P < 0.001$) on the section selected during the previous morning. In most cases, dyads representing selection of the same section on two consecutive mornings occurred more often than expected by chance. Transition matrixes from the Carter Ranch (Table 3) and the Todd Ranch (Table 4) are given as examples. Cows usually stayed in a section for only one day for 72% of the transitions at the Carter Ranch (Figures 1 and 3). In contrast, cows stayed in the same section for at least a week (≥ 7 days) for 53% of the transitions at the Todd Ranch (Figures 2 and 3). Cows stayed in the same section on consecutive days for 93% of the transitions at the Todd Ranch.

At ranches that had relatively gentle topography (Carter, College and Corona), cows stayed in one section for only one day during about 70% of the tracking period (Figure 3). The exception to this was the Corona Ranch during 2011. Cows moved to a new section on the following day for only 31% of the tracking period, and they stayed in the same section for ten or more days during 19% of the tracking period. The precipitation patterns for the Corona Ranch during 2011 differed from 2010 and 2012. In 2011, the amount of winter and spring precipitation (44 mm) was less than that received in 2010 (130 mm) and 2012 (113 mm). Cattle congregated in the swales and draws that finer textured soils and collected more of the very limited water runoff where there was some limited 'green up' of the forage. In 2011, there was virtually no use of half of the sections, while in 2010 and 2012 cattle used all sections.

In the mountain pastures of the Evans and Thackeray Ranches, cattle spent only one day in a section (alternated among sections) for 28% and 53% of the tracking period, respectively. The Thackeray Ranch had by far the smallest sections of the six ranches evaluated (Table 2), and cows often moved between adjacent sections with similar aspect and topography rather than to more distant or topographically different section. Cows at the Evans Ranch remained in the same section for seven or more consecutive days for 15% of the tracking period (Figure 3), and remained in the same section for two to six days for the majority of the tracking period.

In section 1 of the Todd Ranch (mountainous terrain), the Chi-square test indicated that sub-section selected (following morning) was dependent ($P<0.001$) on the sub-section selected during the previous morning. Cows remained in the same sub-section for one day during 35% of the tracking period. Cows remained in the same sub-section for two to three days during 56% of the tracking period, and remained in the same subsection for four to six days during the remaining 9% of the tracking period. Cows spent 11 to 34% of their time in the five sub-sections of section 1.

In section 3 of the Todd Ranch (primarily gentle terrain), there was no evidence that the sub-section selected (following morning) was dependent ($P = 0.83$) on the sub-section selected during the previous morning. Cows spent 60% of their time in one of the five subsections, and 8% to 13% of their time in the other four sub-sections. Cows remained in the same sub-section for only one day during 41% of the tracking period. Cows remained in this sub-section for two to three days, four to six days, and seven to ten days during 32%, 19% and 8% of the tracking period, respectively.

The frequency that cows returned to the same section on consecutive days did not appear to be related to the size of the section (Figure 4). No relationship was detected ($P = 0.15$) between the percentage of days that cows remained in a section for only one day and section size. Similarly, no relationships were detected ($P > 0.10$) between percentage of tracking period and section size for cow remaining in a section for two to three days, four to six days and seven to ten days. However, cows remained in a section for over ten days more often ($P = 0.04$) in larger sections (Figure 4). This relationship was likely influenced by the Todd Ranch where cows remained in the same section for over ten days during 42% of the tracking period, and section size was two times greater than the next largest ranch section.

Discussion

Results of this study support the satiety hypothesis (Bailey and Provenza 2008) prediction that cattle should alternate among feeding sites more frequently in gentle terrain where forages are often more homogeneous than in mountainous terrain where vegetation is diverse because of variation in soils, elevation gradients (Whittaker and Niering 1975) and differences in aspect (Holland and Steyn 1975; Carmel and Kadmon 1999). At the ranches with relatively gentle terrain (Carter, College and Corona Ranches) cows usually changed feeding sites (sections) every day. Such movements would allow cattle to forage in areas with different forage conditions each day, which should facilitate diet mixing and selection of a diverse diet. Based on the Bailey *et al.* (1996) conceptual grazing distribution model, perceived values for sites in homogeneous pastures should be similar to a reference value, which is a moving average of the forage resources that have been encountered during the last few days. Correspondingly, livestock may quickly satiate on a feeding sites because there is little advantage of one feeding site over another (Bailey and Provenza 2008). The Bailey *et al.* (1996) conceptual model also predicts that large herbivores will alternate among homogeneous sites because grazing can quickly reduce the perceived value of a site below the reference value. In rugged terrain, forage is often heterogeneous, and livestock will remain in areas with higher quality forages. Consequently, cattle can more readily mix forages in rugged terrain compared to more homogeneous pastures, and it will likely take longer for animals to become satiated with a feeding site in rough topography than in gentle terrain.

Diet mixing is typically considered a part of diet selection that occurs over time scales of seconds to a few hours. However, feeding site selection allow livestock an opportunity to respond to post-ingestive feedback and select from the same or different availabilities forages by returning to the previous feeding site or moving to a new site. Cattle typically remain in the same feeding site during the evening and morning feeding bouts and then travel to water at the end of the morning grazing bout (Low *et al.* 1981; Bailey *et al.* 1990; Bailey *et al.* 2004). Post-ingestive feedback occurs over periods of minutes to several hours after consumption (Provenza 1995). Thus, animals will have had an opportunity for feedback from the foraging during the previous bout and can use this information for selecting a feeding site when they leave water and being their evening grazing bout. Correspondingly, feeding site selection can facilitate diet mixing at longer temporal scales.

Bailey *et al.* (1990) observed that cattle in a 50-ha pasture in Colorado containing primarily two species of forage were rarely found in the same section of the pasture on two consecutive morning. Sections evaluated in this study were much larger than in the Colorado study. The other study site in the Bailey *et al.* (1990) research was located in Texas, and it was larger in size (248 ha) and contained native rangeland which contained more diverse vegetation than the Colorado pasture. Cows at the Texas site rarely remained in the same section for more than two consecutive mornings.

In 2011, the Corona Ranch was an exception to the regular alternation among feeding sites in gentle terrain. That ranch received very little precipitation during the winter and spring preceding the tracking period, which may have made vegetation on the ranch considerably more diverse during 2011 compared to 2010 or 2012. Most of the pasture probably did not have sufficient soil moisture for plant growth in May and June during the normal growing season for the warm-season grasses that dominate this pasture. The swales and lowlands with finer textured soils were the only areas where there was any noticeable grass growth. Most of the 'green up' occurred in two feeding sites, which effectively changed the Corona Ranch pasture from homogeneous to heterogeneous. Cattle concentrated in feeding sites where there was limited 'green up' and avoided sites with no green forage. Similar behaviour is typical for cattle during 'hot season' grazing of riparian areas where cattle have the choice of uplands with dormant vegetation or actively growing herbage in the riparian areas (DelCurto *et al.* 2005). Cows congregate and remain in areas with higher forage nutritional value. In a small scale Oklahoma study (three-ha pastures), steers alternated among homogeneous patches and focused in patches with more crude protein in a heterogeneous pasture (Bailey 1995).

The Todd Ranch was the largest and most diverse of the ranches studied. Cows usually stayed in the same section for over a week and sometimes up to 30 days. Cows did switch sections but not nearly as often as in the other ranches. All but one of the sections of the Todd Ranch included variable terrain. In the homogeneous section of the Todd Ranch (section 3) there was no pattern in transitions among sub-sections. Cows spent the majority of their time in one sub-section, and movements among sub-sections were equivalent to random selection. In contrast, the sub-section selected in the heterogeneous section of the Todd Ranch that was dependent on the sub-section selected on the previous day. Cows appeared to purposely return to the same subsection for two to three days and then move to another section for the majority of the tracking period. Rugged terrain apparently gave cows the opportunity to graze in different types of areas on different days and likely gave them a greater varieties of forages compared to ranches with gentle terrain. The other mountainous ranches (Evans and Thackeray Ranch) were intermediate between the Todd Ranch and the ranches with gentler terrain (Carter, College and Corona Ranches). The Thackeray Ranch is smaller than the other ranches and virtually all of the pasture is mountainous terrain. Correspondingly, it is somewhat less heterogeneous than Evans and Todd Ranch that contain areas of gentle topography along with mountainous terrain. Feeding site selection patterns at the Thackeray Ranch in this study are similar to those reported in Bailey and Provenza (2008), where they found that cattle rarely stayed in one of the nine sections of the same pasture for more than three consecutive days. Overall, results from this study are consistent with the satiety hypothesis as suggested for both foods and habitats (Provenza 1996; Bailey and Provenza 2008).

Cattle have accurate spatial memories (Bailey *et al.* 1989a; Laca 1998) and can remember the quantity (Bailey *et al.* 1989b) and quality (Bailey and Sims 1998) of -food found in a location. Correspondingly, it is not surprising that cattle can not only remember alternative feedings sites but can compare resource levels encountered at a site they are currently foraging in with other sites in the pasture and use that information in their foraging decisions. Feeding site selection allows livestock increased opportunities to widen diet diversity by moving to new locations with differing forage resources.

Feeding site selection may be a decision process that occurs on an individual basis for beef cattle rather than by a limited number of dominant or leader animals. In herds over 100 cows, the mean association among cows was only 3% in an on-going study conducted by Stephenson and Bailey (2014). Additionally, maximum association levels, or the most associated herd-mate, were relatively low among any two cows grazing within the study pastures. Average maximum associations were only 23% for herd sizes over 100. Although cows prefer to graze with other cows, there does not appear to be any strong associations with any particular herdmate or herdmates. Using tracking data from the College and Corona Ranches, the distance between the two most closely associated cows (pairs) from both the College Ranch and Corona Ranch (a pair of cows from each ranch) were evaluated. The most closely associated collared cows at the College Ranch were separated by over a kilometre and often over two kilometres from each other for 13 of the 33 days of tracking. At the Corona Ranch, the most closely associated of the collared cows spent 14 of the 33 days of tracking over a kilometre from each other. Although the role of social interaction on feeding sites selection are not well understood, animals would be expected to be relatively closely associated if the process were based on a 'leader and many followers' paradigm. The lack of association among cows may be the result of common animal husbandry practices, such as weaning and separation of yearling heifers and two-year-old cows from older cows. In bison, relationships between related females were much stronger when the calves were not weaned (Shaw et al. unpublished data).

Conclusions

Cattle alternate among feeding sites in gentle terrain and correspondingly more homogeneous vegetation conditions. In pastures containing rugged terrain and correspondingly more heterogeneous vegetation, cattle will remain in the same feeding site for longer periods. This regular alternation among feeding sites in gentle terrain and periodic alternation in mountainous areas likely facilitates diet mixing and helps cattle obtain a more diverse diet.

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Figure Captions

Figure 1. Map of the study pasture (4776 ha) at the Carter Ranch located 25 km north of San Simon, Arizona. The pasture was divided into eight sections based on density of locations of 11 cows tracked for 77 days, topographical features and distance to water. Positions of two cows are shown as well as water locations.

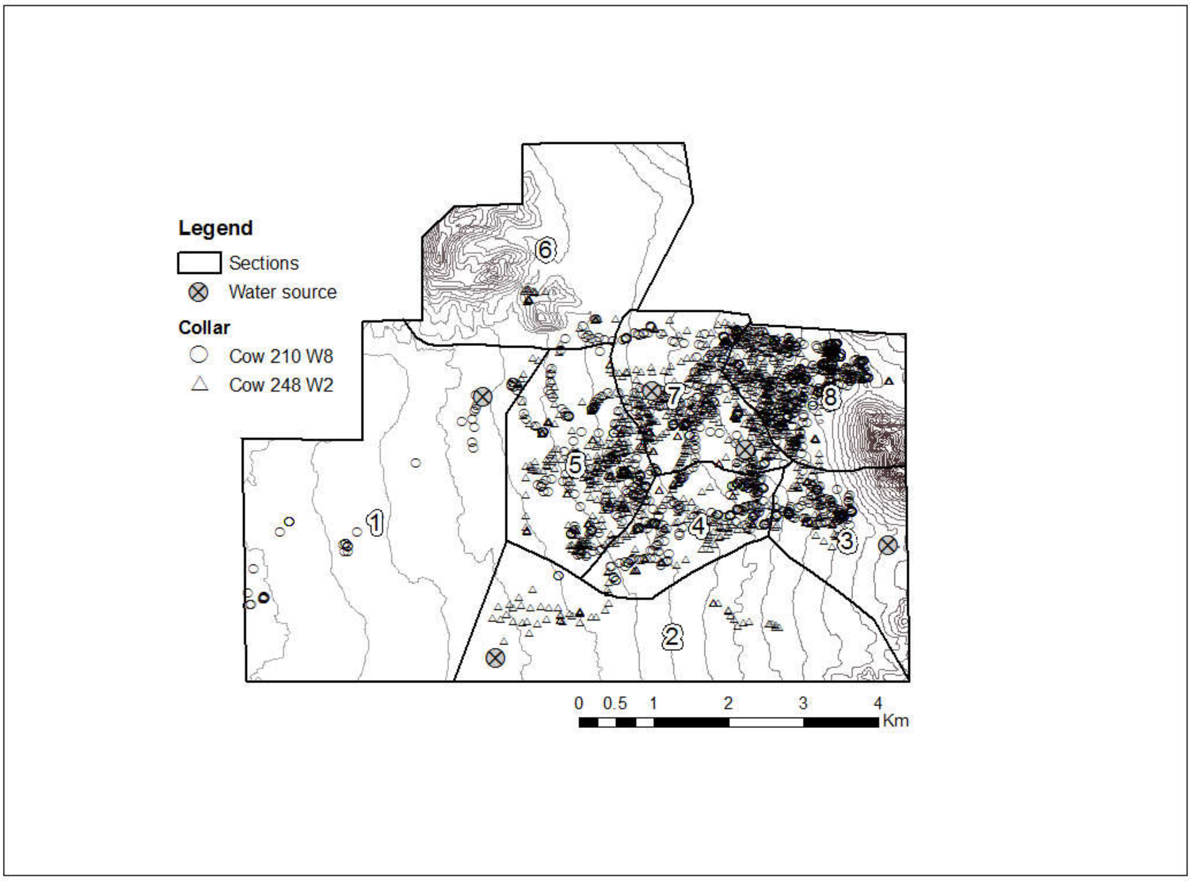

Figure 2. Map of the study pasture (9740 ha) at the Todd Ranch located 11 km northwest of Willcox, Arizona. The pasture was divided into nine sections based on density of locations of 15 cows tracked for 90 days, topographical features, vegetation types and distance to water. Positions of three cows are shown as well as water locations.

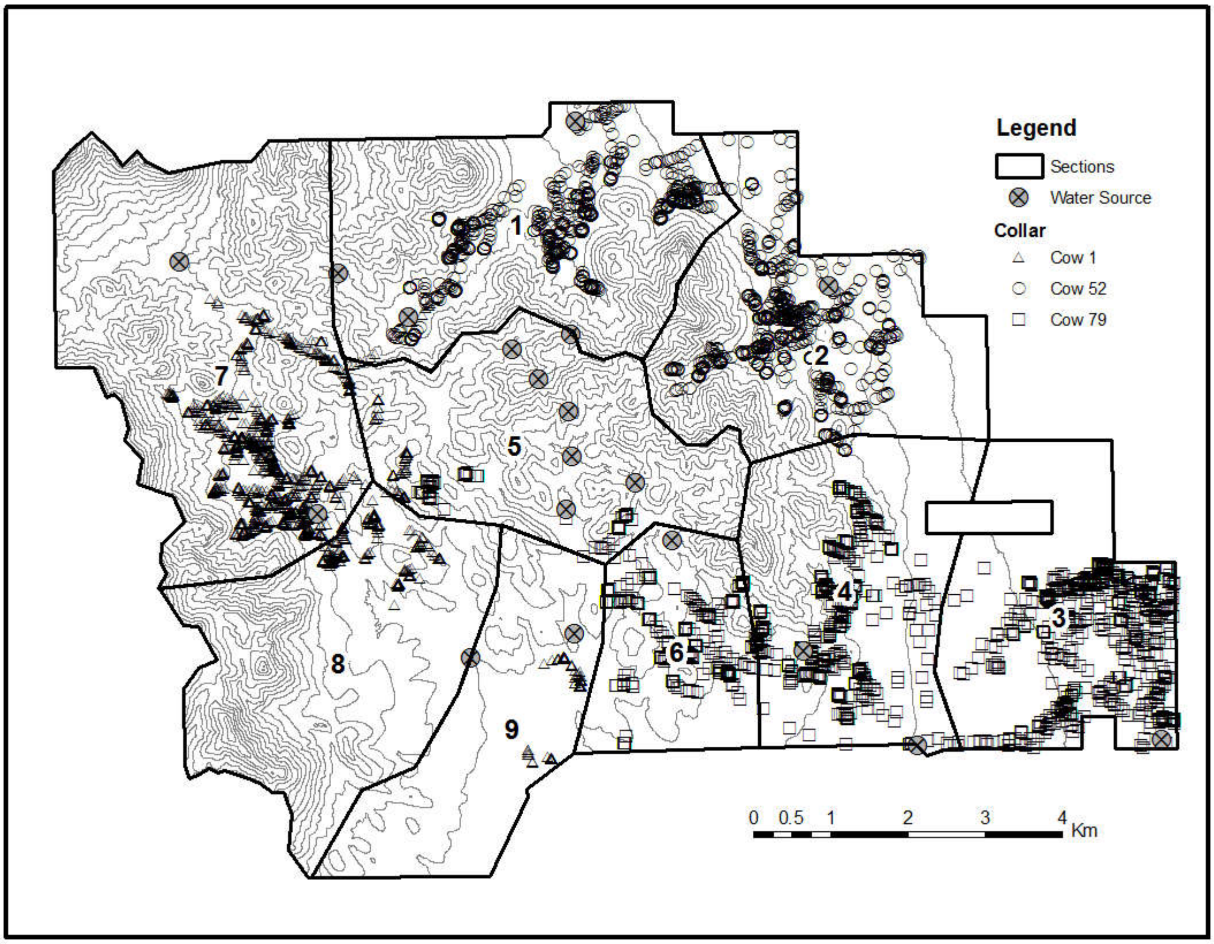

Figure 3. Proportion of tracking period that cows spent in the same section for 1 day (alternate among sections on a daily basis) two to three successive days, four to six successive days, seven to ten successive days and over ten successive days in the same section. Pie diagrams are provided for the Carter Ranch, Chihuahuan Desert Rangeland Research Center (CDRRC or College Ranch), Corona Range and Livestock Research Center (CRLRC or Corona Ranch), Thackeray Ranch and Todd Ranch. Cows were tracked in 2010, 2011 and 2012 at the CRLRC and separate pie diagrams are provided for each year.

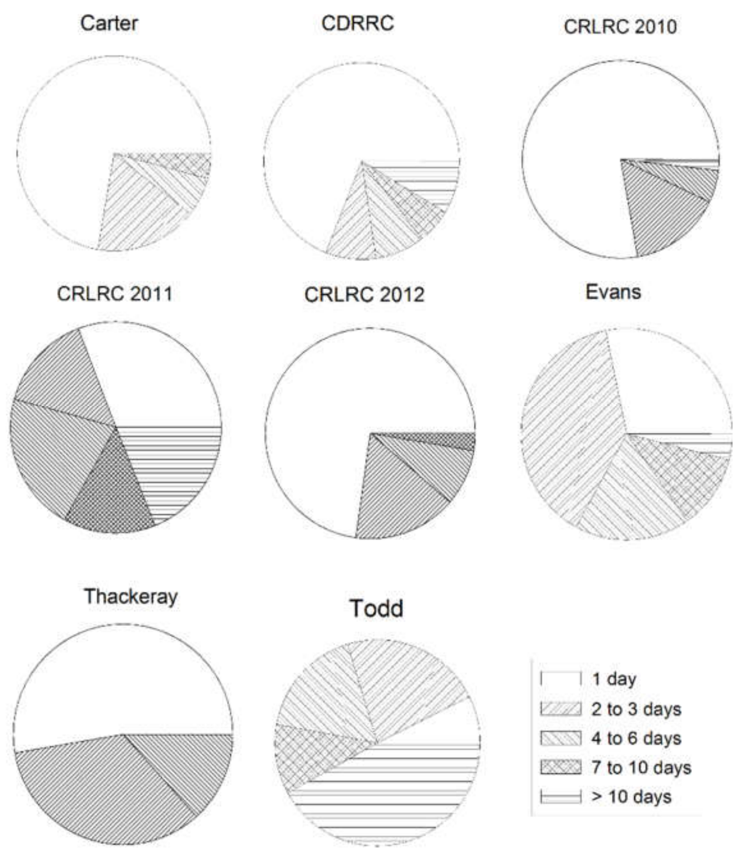

Figure 4. Relationship between the percent of the tracking period that movements among sections occurred every day, two to three days, four to six days, seven to ten days and greater than ten days versus the size of the section (ha). The top graph shows the relationships for all five time periods, while the middle graph shows the relationship between percent of the tracking period that cows moved among sections every day and section size. The bottom graph shows the relationship between percent of the tracking period that cows remained in the same section for ten or more days versus section size. No relationships were detected (*P* > 0.10) between percent of tracking period and section size for the cows remaining in a section for two to three days, four to five days, and seven to ten days.

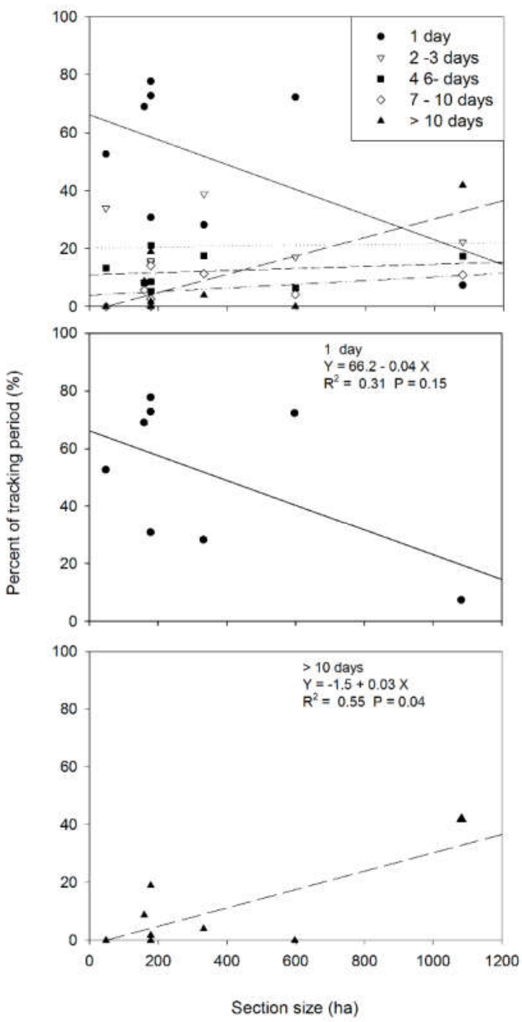

Table 1. Ranch location and description of the abiotic factors that may affect cattle distribution at each ranch.

Ranch	Latitude	Longitude	Terrain	Elevation, m	Slope, %	Maximum distance to water, km	Annual precipitation, mm *
Carter Ranch	32° 29′ N	109° 16′ W	Rolling	1081 - 1250	0 - 29	3.1	137 (249)
College Ranch	32° 31′ N	106° 48′ W	Rolling with arroyos	1250 - 1402	1 - 15	10.0	168 (234)
Corona Ranch	34° 15′ N	105° 27′ W	Rolling	1765 - 1851	0 - 32	4.7	317 in 2010 159 in 2011 134 in 2012 (370)
Evans Ranch	32° 30′ N	108° 31′ W	Rugged and moderate	1670 - 1902	1 - 77	4.8	188 (402)
Thackeray Ranch	48° 21′ N	109° 36′ W	Rugged	1170 - 1400	0-107	1.5	328 (290)
Todd Ranch	32° 15′ N	109° 56′ W	Rugged and gentle	1276 - 2010	1-130	4.8	237 (309)

* Annual precipitation during the year of tracking with the long-term average precipitation in parentheses.

Table 2. Periods of cattle tracking and descriptions of the pastures and the subdivisions into sections for each of the six ranches used in the study.

Ranch	Start Date	End Date	Length of tracking (d)	Pasture Size (ha)	Number of Sections	Mean size of Sections (ha)	Total Cows	Number of GPS-tracked Cows
Corona Ranch	17/5/2010	19/7/2010	63	1601	9	178	120	15
	19/5/2011	22/6/2011	34	1601	9	178	110	13
	28/6/2012	17/8/2012	50	1601	9	178	140	17
College Ranch	29/6/2011	1/8/2011	33	3990	9	159*	43	19
Thackeray Ranch	8/8/2011	14/9/2011	37	336	7	48	213	17
Carter Ranch	21/10/2011	6/1/2012	77	4776	8	597	125	11
Todd Ranch	15/1/2011	15/4/2011	90	9740	9	1082	250	15
Evans Ranch	26/8/2012	14/10/2012	49	1994	6	332	37	16

*Size of sections at CDRRC only includes the extent of areas where GPS-tracked cattle were observed.

Table 3. Transition matrix and Chi-square analysis of sections selected on successive mornings by 11 cows tracked at the Carter Ranch. Observed values represent transitions where cows spent the majority of the morning grazing period (0600 to 1000 h) in a section on successive days.

Previous Section[a]		Following Section[b]							
		1	2	3	4	5	6	7	8
1	Observed	**12**	**0**	**0**	**7**	3	1	1	1
	Expected	**0.7**	2.7	1.6	4.4	5.7	0.4	4.1	5.4
	Chi-Square	**182.1**	2.7	1.6	1.6	1.3	0.9	2.3	3.6
2	Observed	3	**43**	2	26	5	0	11	3
	Expected	2.6	**10.2**	5.8	16.3	21.3	1.5	15.2	20.1
	Chi-Square	0.1	**105.4**	2.5	5.7	12.5	1.5	1.2	14.5
3	Observed	0	6	**12**	5	11	0	10	9
	Expected	1.5	5.8	**3.3**	9.3	12.2	0.8	8.7	11.4
	Chi-Square	1.5	0.0	**23.0**	2.0	0.1	0.8	0.2	0.5
4	Observed	0	31	15	**46**	25	0	7	22
	Expected	4.1	16.0	9.1	**25.6**	33.5	2.3	23.9	31.5
	Chi-Square	4.1	14.0	3.9	**16.2**	2.1	2.3	11.9	2.9
5	Observed	6	6	6	28	**91**	0	28	14
	Expected	5.0	19.6	11.1	31.4	**41.0**	2.8	29.3	38.6
	Chi-Square	0.2	9.5	2.4	0.4	**60.8**	2.8	0.1	15.7
6	Observed	1	0	0	0	4	**3**	0	3
	Expected	0.3	1.2	0.7	1.9	2.5	**0.2**	1.8	2.4
	Chi-Square	1.5	1.2	0.7	1.9	0.9	**45.8**	1.8	0.2
7	Observed	1	1	3	17	28	3	**47**	35
	Expected	3.8	14.8	8.4	23.7	31.0	2.1	**22.1**	29.1
	Chi-Square	2.1	12.9	3.5	1.9	0.3	0.3	**28.2**	1.2
8	Observed	0	3	13	15	21	6	30	**90**
	Expected	5.0	19.5	11.1	31.3	40.8	2.8	29.1	**38.4**
	Chi-Square	5.0	14.0	0.3	8.5	9.6	3.6	0.0	**69.2**

[a] Section that a tracked cow was observed on day *x*.

[b] Section that a tracked cow was observed on day *x + 1*

Overall Chi-square = 731.2, df = 49, $P < 0.001$

Table 4. Transition matrix and Chi-square analysis of sections selected on successive mornings by 15 cows tracked at the Todd Ranch. Observed values represent transitions where cows spent the majority of the morning grazing period (0600 to 1000 h) in a section on successive days.

Previous Section[a]		Following Section[b]								
		1	2	3	4	5	6	7	8	9
1	Observed	**100**	7	0	0	0	0	1	0	0
	Expected	**8.6**	15.9	16.9	10.2	4.2	9.2	6.3	21.3	15.4
	Chi-Square	**966.0**	5.0	16.9	10.2	4.2	9.2	4.5	21.3	15.4
2	Observed	7	**185**	0	6	0	0	0	0	0
	Expected	15.8	**29.2**	30.9	18.8	7.6	16.9	11.6	39.0	28.2
	Chi-Square	4.9	**831.8**	30.9	8.7	7.6	16.9	11.6	39.0	28.2
3	Observed	0	0	**172**	32	0	3	0	0	0
	Expected	16.6	30.5	**32.4**	19.6	8.0	17.6	12.1	40.8	29.4
	Chi-Square	16.6	30.5	**602.8**	7.8	8.0	12.1	12.1	40.8	29.4
4	Observed	0	7	35	**80**	1	5	0	0	0
	Expected	10.2	18.9	20.0	**12.1**	4.9	10.9	7.5	25.2	18.2
	Chi-Square	10.2	7.5	11.2	**379.5**	3.1	3.2	7.5	25.2	18.2
5	Observed	0	0	1	0	**38**	8	3	0	2
	Expected	4.2	7.7	8.1	4.9	**2.0**	4.4	3.0	10.2	7.4
	Chi-Square	4.2	7.7	6.3	4.9	**646.9**	2.9	0.0	10.2	3.9
6	Observed	0	0	3	10	8	**80**	0	0	16
	Expected	9.4	17.2	18.3	11.1	4.5	**10.0**	6.8	23.1	16.6
	Chi-Square	9.4	17.2	12.8	0.1	2.7	**492.1**	6.8	23.1	0.0
7	Observed	1	0	0	0	2	0	**66**	7	2
	Expected	6.2	11.5	12.2	7.4	3.0	6.6	**4.6**	15.4	11.1
	Chi-Square	4.4	11.5	12.2	7.4	0.3	6.6	**826.9**	4.6	7.5
8	Observed	0	0	0	0	0	2	8	**200**	57
	Expected	21.4	39.4	41.7	25.3	10.3	22.7	15.6	**52.6**	38.0
	Chi-Square	21.4	39.4	41.7	25.3	10.3	18.9	3.7	**412.9**	9.5
9	Observed	0	0	0	0	3	17	1	59	**115**
	Expected	15.6	28.7	30.5	18.5	7.5	16.6	11.4	38.4	**27.7**
	Chi-Square	15.6	28.7	30.5	18.5	2.7	0.0	9.5	11.0	**274.6**

[a] Section that a tracked cow was observed on day *x*.

[b] Section that a tracked cow was observed on day *x + 1*

Overall Chi-square = 6364.9, df = 64, $P < 0.001$