Distribution and abundance of ticks infesting livestock population along Karakorum highway from Mansehra to Gilgit, Pakistan

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Distribution and abundance of ticks infesting livestock population along Karakorum highway from Mansehra to Gilgit, Pakistan

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ABSTRACT. Ticks and tick-borne infections pose major economic threats to the livestock industry throughout the world. The present study reports the point prevalence of ticks in the free range livestock population of the plain and hilly areas of Khyber Pakhtunkhwa (Mansehra, Haripur, Shangala, Kohistan), and Gilgit Baltistan (Diamer, Gilgit, Astor) along the Karakoram highway. Through convenient and snowball sampling techniques, a total of 813 animals, consisting of 232 sheep, 163 cattle, 365 goats and 53 buffaloes were screened for their tick burden. During the study, the two tick species identified were *Hyalomma anatolicum* and *Rhipicephalus microplus*. The overall prevalence of tick infestation among the screened livestock was 75.03%, with the highest distribution in sheep (81.47%) followed, in order, by cattle (77.91%), goats (72.05%) and buffalo (58.49%). The district-wise prevalence of ticks was the highest in Haripur (85.58), followed, in order, by Gilgit (83.10%), Mansehra (81.14%), Batagram (81.05%), Shangala (77.78%), Kohistan (75.38%), Diamer (72.28%) and Astor (32.22%). The prevalence of ticks was found to be higher (85.67%) in younger livestock than adults (66.44%), and in females (80.33%) than males (66.44%). The present study provides the first report of the tick distribution in higher altitudes of northern Pakistan and confirms the presence of *Hyalomma* and *Rhipicephalus* ticks in the plains, as well as the hilly geoclimates of Pakistan. Furthermore, the data on risk factors allows us to make recommendations to restructure the existing husbandry system of northern areas of Pakistan with the aim of reducing the tick burden on livestock.

Keywords: Ticks; Khyber Pakhtunkhwa; Gilgit- Baltistan; Pakistan; *Hyalomma anatolicum*; *Rhipicephalus microplus*

INTRODUCTION

Ticks (Acarina: Ixodidae), blood imbiping ectoparasites of mammals, birds and reptiles, have an epidemic dissemination in tropical and sub-tropical regions (Gaisuddin et al., 1994; Vesco et al., 2011). Ticks are prevalent worldwide from Asia (Haque et al., 2011; Bilkis et al., 2011; Sajid et al., 2011; Razmi and Ramoon, 2012; Singh and Rath, 2013), Africa (Reye et al., 2012; Tiki and Mekonnen, 2011; Elghali and Hassan, 2012), North and South Americas (Guimaraes et al., 2001; Lohmeyer et al., 2011), Australia (Springell, 1974; Kamau, 2011) and Europe (Kirby et al., 2004; Scharlemann et al., 2008). Ticks not only cause direct losses, but also act as vectors for various pathogens of bacterial, rickettsial, protozoal, and viral origin (Petney et al., 2007). The direct production losses caused by ticks include loss of milk production, reduced weight gain (Peter et al., 2005; Sajid et al., 2007), low quality skins and hides (Jongejan and Uilenberg, 2004), and mortality (Niyonzema and Kiltz, 1986). Besides these production losses, ticks also cause clinical and sub-clinical infections such as anemia, dermatitis, paralysis, otocarriasisis (Drummond, 1983; FAO, 1998) and secondary bacterial infections (Ambrose et al., 1999). Various diseases vectored by ticks are babesiosis, theileriosis, anaplasmosis, lyme

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disease, tick typhus, Rocky Mountain spotted fever and Crimean-Congo haemorrhagic fever (Otim, 2000; Bell-Sakyi et al., 2004). During the last three decades tick-borne infections have increased globally (Patz et al., 2005). Production and economic losses are proportional to the tick burden on the body of host, which results in increased irritation, restlessness, weight loss and disease transmission (Gosh et al., 2007; Agarwal and Gupta, 2010). It has been estimated that economic losses due to vector transmitted diseases and cost of tick control worldwide is 7.0 billion dollars annually (Harrow et al., 1991; Garcia, 2003).

The distribution of ticks in any region is closely associated with certain biotic and abiotic features (Sonenshine, 1993). Tick dispersal in any area depends upon the environmental factors (Estrada-Peña, 2003) e.g. temperature of 27-39 °C and relative humidity range of 60-80% render ticks more active (Rodriguez and Dominguez, 1998); however, ticks can also survive at temperatures down to -18.5˚C (Clark, 1995; Vandyk et al., 1996, Schulze et al., 2001). In the past few decades, due to global warming, ticks have been reported in areas of higher altitudes which were previously tick-free. In Pakistan, studies conducted on prevalence of tick species across the country report the frequency distribution within the range of 6.99 to 80% in small and large ruminant population. However, studies on the tick distribution in the northern areas of Khyber Pakhtunkhwa (KPK) and Gilgit Baltistan (GB) are not available except a single study by Khan (1993) in Kaghan valley, almost two decades ago. The present study was aimed to explore the northern area of Pakistan for the distribution of tick fauna in livestock population.

MATERIALS AND METHODS

Study Area

The present study was conducted in selected areas of the provinces of KPK and GB including: Haripur (33.988 °N 72.95 5°E), Mansehra (34°20′N 73°12′E), Shangala and Batagram (34.41°N 73.1°E), Kohistan (34° 54′ and 35° 52′ N and 72°43′ and 73°57′ E), Astor (35° 22′ N, 74° 51′ E) and Gilgit (35°55′19″ N 74°18′31″ E). The average distance between each study area ranged from 30 to 100 kilometers. In these areas, animals are reared under a traditional management system (i.e. farmers followed practices of their forefathers and deal with animals according to traditional beliefs and knowledge) in which the livestock is entirely dependent upon grazing. Variation in temperature, rainfall, and humidity levels of the study districts depends upon the differences in the landscape, climate and elevation of these areas from sea level (Anonymous, 2011). The present study was conducted during June which is the hottest month of summer season in Pakistan.

Selection of Animals

Convenience and snowball sampling techniques were applied in order to select the sample animals/farms along the Karakoram Highway screened during this study. A questionnaire was designed to acquire essential information relating to animals (sex, age and species), qualitative and quantitative abundance of ticks and/or other parasites and the environmental conditions, including management (Thrusfield, 2007).

Collection and Identification of Ticks

For collection of ticks, the whole body of the animal was screened. Ticks were removed with the help of a fine tweezer with minimum damage to the mouth parts (Soulsby, 1982), transferred to McCartney sample collection bottles containing 70% ethanol and labelled appropriately. After collection, specimens were brought to the Department of Parasitology, Faculty of Veterinary Science, University of Agriculture, Faisalabad, Pakistan for taxonomic identification. Ticks were identified using stereomicroscope (IM-SZ-500 IRMECO Germany) according to standard keys (Walker et al., 2007).

Statistical Analyses

Prevalence and association of determinants was analyzed by using multivariate analysis (multiple logistic regressions) and odds ratio. Pairwise comparison was carried out by keeping buffaloes (animal species), Rhipicephalus spp. (tick species), males (sex), adults (age) and the Astor district (area) in group 2 of the analysis (Schork and Remington, 2010). All statistical analyses were conducted using SAS software package (SAS, 2010).

RESULTS

The overall prevalence of tick infestation in the
were not found to be statistically associated (P>0.05) with the tick distribution in the study districts. Table 1 details the distribution of ticks by individual variables. Table 3 depicts the distribution of the two species of hard ticks infesting livestock in the various districts of KPK and GB.

**DISCUSSION**

The prevalence of tick infestation in ruminants livestock population of the study area was found to be 75.03% (610/813) with a higher (P>0.05) tick distribution in KPK than in GB. Only adult ticks of *Hyalomma anatolicum* and *Rhipicephalus microplus* were present on the screened livestock population. Animals/livestock species wise prevalence of ticks were 81.47% in sheep, 77.91% in cattle, 72.05% in goats and 58.49% in buffaloes. Similarly, animal numbers found positive for ticks species were 309 and 301 with *Hyalomma* and *Rhipicephalus* spp. respectively. A total of 18907 adult ticks were collected from the four livestock species in the study areas. Higher number of ticks were collected from sheep (7590), followed in order by goats (6622), cattle (4004), and buffaloes (691). Distribution of ticks collected from the screened livestock species is given in Table 2. Tick distribution was found highest (P<0.05) in the Mansehra district followed by the Haripur, Batagram, Shangala, Kohistan, Diamer, Gilgit and Astor districts. Host age and sex

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### Table 1. Frequency distribution of hard ticks (Ixodidae) in different livestock species of Khyber Pakhtunkhwa and Gilgit-Baltistan, Pakistan

<table>
<thead>
<tr>
<th>Variables</th>
<th>Levels</th>
<th>Animals Screened</th>
<th>Tick Positive</th>
<th>Prevalence (%)</th>
<th>95% Confidence interval</th>
<th>Odds Ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower limit</td>
<td>Upper limit</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Animal Species</td>
<td>Sheep</td>
<td>232</td>
<td>189</td>
<td>81.47</td>
<td>76.07</td>
<td>86.06</td>
<td>1.39</td>
</tr>
<tr>
<td></td>
<td>Cattle</td>
<td>163</td>
<td>127</td>
<td>77.91</td>
<td>71.06</td>
<td>83.78</td>
<td>1.33</td>
</tr>
<tr>
<td></td>
<td>Goats</td>
<td>365</td>
<td>263</td>
<td>72.05</td>
<td>67.28</td>
<td>76.48</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td>Buffalo</td>
<td>53</td>
<td>31</td>
<td>58.49</td>
<td>44.94</td>
<td>71.13</td>
<td>-</td>
</tr>
<tr>
<td>Tick Species</td>
<td><em>Hyalomma</em></td>
<td>813</td>
<td>309</td>
<td>38.01</td>
<td>34.72</td>
<td>41.38</td>
<td>1.03</td>
</tr>
<tr>
<td></td>
<td><em>Rhipicephalus</em></td>
<td>813</td>
<td>301</td>
<td>37.02</td>
<td>33.75</td>
<td>40.39</td>
<td>-</td>
</tr>
<tr>
<td>Sex</td>
<td>Female</td>
<td>483</td>
<td>388</td>
<td>80.33</td>
<td>76.61</td>
<td>83.69</td>
<td>1.19</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>330</td>
<td>222</td>
<td>67.27</td>
<td>62.07</td>
<td>72.18</td>
<td>-</td>
</tr>
<tr>
<td>Age</td>
<td>Young</td>
<td>393</td>
<td>311</td>
<td>79.13</td>
<td>74.90</td>
<td>82.94</td>
<td>1.11</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>420</td>
<td>299</td>
<td>71.19</td>
<td>66.72</td>
<td>75.37</td>
<td>-</td>
</tr>
<tr>
<td>Province</td>
<td>KPK</td>
<td>498</td>
<td>403</td>
<td>80.92</td>
<td>77.29</td>
<td>84.74</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td>GB</td>
<td>315</td>
<td>207</td>
<td>65.71</td>
<td>60.34</td>
<td>70.80</td>
<td>-</td>
</tr>
<tr>
<td>Districts</td>
<td>Manshera</td>
<td>162</td>
<td>132</td>
<td>81.14</td>
<td>74.94</td>
<td>86.91</td>
<td>2.53</td>
</tr>
<tr>
<td></td>
<td>Haripur</td>
<td>104</td>
<td>89</td>
<td>85.58</td>
<td>77.82</td>
<td>91.38</td>
<td>2.66</td>
</tr>
<tr>
<td></td>
<td>Batagram</td>
<td>95</td>
<td>77</td>
<td>81.05</td>
<td>72.24</td>
<td>88.00</td>
<td>2.52</td>
</tr>
<tr>
<td></td>
<td>Shangala</td>
<td>72</td>
<td>56</td>
<td>77.78</td>
<td>67.11</td>
<td>86.25</td>
<td>2.41</td>
</tr>
<tr>
<td></td>
<td>Kohistan</td>
<td>65</td>
<td>49</td>
<td>75.38</td>
<td>63.86</td>
<td>84.69</td>
<td>2.34</td>
</tr>
<tr>
<td></td>
<td>Diamer</td>
<td>83</td>
<td>60</td>
<td>72.28</td>
<td>61.95</td>
<td>81.10</td>
<td>2.24</td>
</tr>
<tr>
<td></td>
<td>Gilgit</td>
<td>142</td>
<td>118</td>
<td>83.10</td>
<td>76.26</td>
<td>88.60</td>
<td>2.58</td>
</tr>
<tr>
<td></td>
<td>Astor</td>
<td>90</td>
<td>29</td>
<td>32.22</td>
<td>23.19</td>
<td>42.38</td>
<td>-</td>
</tr>
</tbody>
</table>

### Table 2. Tick Abundance in Screened Livestock Species of Gilgit Baltistan and Khyber Pakhtunkhwa, Pakistan

<table>
<thead>
<tr>
<th>Sr. No.</th>
<th>Livestock species</th>
<th>Range of tick Burden</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Minimum</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>Sheep</td>
<td>6</td>
<td>145</td>
</tr>
<tr>
<td></td>
<td>Cattle</td>
<td>25</td>
<td>125</td>
</tr>
<tr>
<td></td>
<td>Goats</td>
<td>19</td>
<td>130</td>
</tr>
<tr>
<td></td>
<td>Buffaloes</td>
<td>10</td>
<td>60</td>
</tr>
</tbody>
</table>
is much higher in the developing countries of Asia (Siddqi and Jan, 1986; Khan et al., 1993; Sajid et al., 2007, 2009, 2011; Yi-Lun et al., 2011; Iqbal et al., 2013; Ali et al., 2013; Sultana et al., 2015) and Africa (Walker and Koney, 1999; Walker, 2003), where control measures are infrequently applied, than in Australia (Springell, 1974; Kamau, 2011), Europe (Papadopoulos et al., 1996; Hostis and Seegers, 2002) and the Americas (Guimaraes et al., 2001; Lohmeyer et al., 2011). Extensive research studies have been conducted on the prevalence of the tick fauna and associated risk factors in various districts of Pakistan. Seven tick species have been reported from sixteen districts of Pakistan, with a prevalence ranging from 6.99% to 86.50% in the bovine and caprine populations of various study areas during 1971 to 2015 (Iqbal et al., 1971; Khan et al., 1993; Zaman, 1997; Kakar and Kakarsulemankhel, 2008; Sajid et al., 2008; Durrani and Shakoori, 2009; Irshad et al., 2010; Perveen, 2011; Atif et al., 2012; Ali et al., 2013; Iqbal et al., 2013; Tasawar et al., 2014; Mustafa et al., 2014; Sultana et al., 2015). However, the northern areas of the country have been ignored due to harsh climate and the very difficult access to small holder animal farmers in the remote hilly villages. This is the first attempt to conduct such a study in these areas. The two tick species, i.e. *H. anatolicum* and *R. microplus*, which were identified from the screened livestock population along the Karakaram highway, have also been reported earlier from other parts of the country (Ali, 1988; Khan et al., 1993, 1996; Wahid et al., 2004; Durrani, 2008; Sajid et al., 2008; Irshad et al., 2010; Atif et al., 2012; Iqbal et al., 2013; 2014; Mustafa et al., 2014; Tasawar et al., 2014). These two tick species have also been reported to infest deer, equine, swine, canine and humans. Further, these two ticks have been reported as vectors for *Staphylococcus* spp., *Coxiella burnetti*, tick-borne encephalitis virus, and *Ehrlichia* spp. (Yang et al., 1993; Anbalagan et al., 2014), Prevalence of these species of ticks has already been reported in wide range of farm animals from the hilly and plain areas of Malaysia (Mariana et al., 2008). The results of present study indicate a relatively higher prevalence of ticks in the livestock populations of the plain and hilly areas of Pakistan as compared to...
Season plays a vital role in the tick distribution as has been reported from all over the globe with the highest prevalence observed during warmer months. Higher humidity is not favorable for ticks, as it also affects the questing behavior of ticks. Studies have shown that changes in temperature, soil moisture, and cloud cover can influence tick activity, primarily due to the fact that ticks must remain active to find a host. It has been reported (Greenfield, 2011) that tick growth and development is controlled by the amount of time a tick can spend questing, which in turn is an important determinant of tick survival. Humidity and temperature also have a profound effect on tick activity, primarily because they affect the desiccation of ticks, thus reducing tick abundance. In addition, tick survival and activity are dependent on other factors, such as vegetation height. A humidity of above 80% is essential for tick survival, and levels below this have a detrimental effect on tick survival (Macleod, 1934, 1935; Milne, 1948). It is therefore believable that humidity plays a significant role in tick survival (Macleod, 1934, 1935; Milne, 1948). Ticks usually move in search of a host when temperatures increase (Macleod, 1934, 1935; Milne, 1948). Tick activity is greatly affected by changes in temperature. It has been reported that at temperatures <7°C, ticks remain inactive, only venturing out of the mat and up the vegetation to quest for a host when temperatures increase (Macleod, 1939). Further, an increase in temperature not only causes an increase in the distribution of ticks but is also linked to the encroachment of ticks into higher altitudes not previously colonized by ticks (Danielov et al., 2008). The increase and decrease in temperature is also associated with tick diapause and shift in nymph and adult activity. It is reported that lower temperatures (16.0–20.9°C) significantly reduce the number of ticks recovered during dragging. Increase and decrease in temperature, soil moisture, and cloud coverage can also affect tick questing. Studies have shown that higher humidity is not favorable for ticks, as they become prone to over saturation, thus limiting their activities (Lee, 1946; Milne, 1948; Arthur, 1962). Gray (2002) reported that vegetation structure plays a large role in the presence and the absence of ticks. Ticks are often recorded in woodland habitats, as these provide a dense shrub layer; habitat with bracken, however, will also provide a suitable habitat. Vegetation height is also an important factor which affects tick prevalence, as higher heights are associated with a decrease in tick abundance. It is reported that the tick abundance is higher at 151-300mm high vegetation. Presence and absence of host in an area also affect occurrence of ticks. So, presence of ticks is not static as it depends on a number of factors.

The reasons of high prevalence of ticks in the livestock population nurtured along the Karkoram highway of Pakistan could be due to different factors. Geography and climate of the area are among those factors which are linked with variables such as: temperature, rainfall, humidity, vegetation, landscape and altitude and the role of these factors leading to a higher abundance of ticks has been reported (Estrada-Pena, 2003). Recently, it has been reported that the height of the study area from the sea level has negative correlation with the tick distribution and abundance (Qviller et al., 2013). Probably, at the higher altitudes, environmental temperature does maintain the optimum range required for the growth and development of ticks (Perret et al., 2000; Jouda et al., 2004; Randolph, 2004). Further, at higher altitudes, the microclimatic conditions diminish the body reserves of the ticks, which ultimately lead to delayed embryogenesis (Daniel, 1993). During the past decade, increases in the climatic temperature might have resulted in the higher abundance of ticks even at higher altitudes (Burri et al., 2007; Cadenas et al., 2007). Climate alteration is a believable justification for changes in the distribution and severity of tick infestation at higher altitude (Coulson et al., 2009). In other words, environmental changes favor settlement of ticks at higher altitudes where they had not colonized earlier (Danielova et al., 2008). Vegetation and forest make another microclimatic component of the area that have a significant role in higher distribution of ticks as it provides covering layer for lodging of ticks (Gray, 2002). Hilly areas of GB and KPK are densely shielded by shrubs, bushes and forests which provide appropriate resources for the exophiliic questing behavior of ticks.

Season plays a vital role in the tick distribution as has been reported from all over the globe with highest prev-
alcence in summer (Singh and Singh, 1999; Hussain and Kumar, 1991; Vatsya et al., 2008; Haque et al., 2011). In Pakistan too, summer season has been reported most favorable for the growth, propagation and infestation of ticks on the livestock population from various regions of the country (Sajid et al., 2007; Durrani and Shakoori, 2009; Sajid et al., 2009, 2011; Atif et al., 2012; Iqbal et al., 2013) Current point prevalence was determined in the summer when the weather conditions are hot and humid which favour tick growth and development (Gosh et al., 2007). Probably, nomadism also contributes towards higher distribution of tick infestation in the area as in our country animal keepers/farmers from the warmer areas of Punjab, Sindh and KPK migrate with their livestock in summer season to the hilly areas like GB where temperature is much lower during summer season. This activity favours successful transmission of ticks from the immigrant livestock to the indigenous animals of the area.

Husbandry practices are also correlated with tick abundance and distribution. In this context, mixed grazing of different animal species on the same pasture and/or mixed housing provides maximum opportunity to ticks to infest a large population at one time. In Pakistan, animal sheds are made of bricks and stones with mud which provides cracks and crevices that is suitable for the nidiculous questing behaviour of ticks (Soulsby, 1982). Lack of awareness about the treatment of infested animals and lack of veterinary facilities are also noteworthy reasons for the higher tick infestation in these areas. Most of the interviewed farmers were illiterate and had a misconception that ticks do not impact on animal health and production. On the basis of the results of the present study, some recommendations for farmers and researchers are: (a) prophylactic treatment of the livestock populace must be administered at the start of warm season (March-April) (b) young and female animals need extra care (c) dairy and livestock development organizations must plan an awareness campaign in these areas to explain the possible threats of ticks and tick-borne diseases to the livestock. The present study is the first report of the successful adaptation and settlement of ticks at the high altitudes of northern Pakistan.

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REFERENCES

Agarwal P, Gupta AR (2010) Management of ectoparasites of livestock. Department of Medicine, QU-AF-Bhubaneswar, Orissa, India.


Anonymous (2011) Pakistan Meteorological Department, Lahore, Pakistan.


MacLeod J (1934) *Ixodes ricinus* in relation to its physical environment, the influence of climate on development. Parasitology 26: 282–305.


