Oviposition site selection by *Gasterophilus pecorum* (Diptera: Gasterophilidae) in its habitat in Kalamaili Nature Reserve, Xinjiang, China

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Abstract – Oviposition site selection is an important aspect of the behavioural ecology of insects. A comparison of the habitats used by a species enhances our understanding of their adaptation to altered environments. We collected data on the oviposition behaviours of *Gasterophilus pecorum* (Diptera: Gasterophilidae) in its habitat in Kalamaili Nature Reserve (KNR), Xinjiang, China between March and October 2014. We found 91 quadrats were used by *G. pecorum* for oviposition. Examining 13 ecological factors using the *t*-test, chi-square test, and principal component analysis showed that *G. pecorum*’s oviposition habitat was preferentially on slopes with inclinations of 10–30° that were semi-sunny, semi-cloudy slopes, in positions high or low on the slopes, with preferences for total plants lower than 10% and *Stipa capillata* coverage lower than 10% on the low slopes, but *Ceratoides latens* coverage on the high and intermediate slopes, when the numbers of plant species and families were lower than five. *G. pecorum* often selected sites at a distance < 2000 m from a water source and average altitude 900–1000 m. The oviposition site selection by *G. pecorum* may be correlated with the behaviour of Przewalski’s horses (*Equus ferus przewalskii*), and water and food resources may strongly influence oviposition site selection, as Przewalski's horses rest and forage in these areas.

Key words: Przewalski’s horses, Oviposition site, *Gasterophilus pecorum*, Kalamaili Nature Reserve.

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Introduction

Horses and other equines are hosts to the larvae of the *Gasterophilus* species causing gastrointestinal myiasis [23]. They are prone to *Gasterophilus* infections because the pastures where they graze are contaminated with infective stages (eggs and larvae) of *Gasterophilus*, resulting in continuous infestation and re-infection. Parasites can have various effects on the health [43, 47, 51, 60] and behaviour [26, 48] of their hosts. Several carefully controlled studies suggest that host mortality rates increase with parasite burden, while the fecundity of infested hosts decreases significantly [30]. Therefore, it is important to examine the ecological factors that determine parasite loads, including environmental factors (climate, humidity, temperature, rainfall, vegetation, stocking density, and management) [41, 44], and the feeding, movement, and defecation patterns of the host, which determine the parasites encountered [26, 31]. Przewalski’s horse, which was listed as endangered by the International Union for Conservation of Nature in 2011, was once distributed widely in the Eurasian desert steppe; however, it became extinct in the wild in the middle of the last century [5, 35], with a few remnant populations existing as small captive breeding herds in western countries [29]. Efforts to reintroduce Przewalski’s horse in Central Asia, Mongolia, Russia, and north-western China started in the 1990’s [29]. In northwest China, Przewalski’s horses were released into the Kalamaili Nature Reserve (KNR) in Xinjiang in August 2001, and the population has subsequently increased significantly [28, 30, 59].

Movement strategies are crucial for the survival of animals that need to find resources or escape from predators or parasites [34, 54]. *Gasterophilus pecorum* is the dominant botfly species and aggressively attacks horses in the KNR and accounts for the vast majority of all parasites infecting them [28, 30, 34]. In addition, the oviposition sites of *G. pecorum* differ from those of other botflies. *G. pecorum* mainly lays its eggs on grass, while other species lay their eggs on horse hair, forelegs, lips, face and the intermandibular area [61]. Although deworming is performed annually during the winter in these Przewalski’s horses, recurring *Gasterophilus* infections remain prevalent and the parasitic burden is severe with an infection rate of 100% [30]. *Gasterophilus pecorum* was the dominant species and was found to aggressively attack equids in the KNR and to account for the vast majority of all parasites infecting equids [30]. In contrast, research reports that *Gasterophilus intestinalis* and *Gasterophilus nasalis* are the dominant species in other regions of the world [38, 61]. What has caused this? Where are the oviposition sites of *G. pecorum*? No study has examined this so far. The distribution of water [46] and food resources [18] has a major impact on the movement patterns of many large herbivores, particularly equids. The movement of host animals may also affect *Gasterophilus* life cycles. The distribution of both host and parasite is crucial, as the population sizes and their interconnections determine co-evolutionary outcomes [4, 10]. The spatial distributions and co-evolution of parasites and hosts usually overlap completely [6]. Research on parasitological examinations in the three equid species shows how the factors home range, social structure, and resource selection, significantly impact parasitic burden [39]. Species of *Gasterophilus* are obligate parasites of animals like horses, donkeys, and mules in their larval stage of the life cycle [55]. A large number of eggs can be laid by the female fly, and the eggs of various species differ in colour and laying location in the host body. In *G. pecorum* the eggs are laid in batches of 10–115 and distributed on pasture vegetation. The eggs are easily observable and hatch spontaneously in about 3–9 days. In *G. pecorum* eggs hatch within 3 to 5 min in the mouth [60].

During warm months, Przewalski’s horses move to high, bare places where there is no forage during the warmer hours of the day. They likely move to escape flies, although the flies tend to follow [26]. *G. pecorum* has distribution in Europe, Africa, and Asia, and its common names are bottflies and dark-winged horse bot [60]. Large numbers of attached larvae can cause inflammation, hinder swallowing, and may eventually lead to death resulting from constriction of the oesophagus [55]. In Mongolia, only one fly belonging to *Gasterophilus* was found [26], and at times none were observed [39]. The reason for the differences in the level of infection between China and Mongolia remains unknown. It is possible that the level of *G. pecorum* infection in Przewalski’s horses is associated with the unique geographic environment [57]. The features of natural conditions and biological combinations are extremely arid and semi-arid desert in KNR. KNR and Tashikuergannature reserve in Xinjiang with desert plateau characteristics are typical of similar kinds of areas in China and elsewhere in the world. This position was the ancient ecological corridor for the Eurasian continent and is the ancestral home of Przewalski’s horses.

When studying the effects of changes in host numbers and population structure on disease spread and persistence, one needs to consider variation in the life histories of the parasites [19]. The selection of oviposition habitat evolves to ensure parasitic reproduction. Adult *Gasterophilus* spp. lay eggs during specific seasons of the year in most regions of the world [15]. Some monitored studies show egg-laying activity with a bimodal trend with a higher first peak in October–November that decreases suddenly from December to January, although different breeding conditions can significantly affect the average number of eggs laid [41]. Many studies have examined egg laying in bottflies, most have focused on when the eggs are laid and the relationship between oviposition and local climate [52]. To our knowledge, some studies have examined the specific location of oviposition in *Gasterophilus* [15, 41]. However, these results did not include *G. pecorum* and did not describe the egg position and habitat features in detail, especially the specific geographical environment in China’s Xinjiang where three kinds of sympatric equines live. Therefore, this study first examined *G. pecorum* oviposition habitat selection, and then compared it with wild horse habitat selection and behaviour, to identify why *G. pecorum* has become the dominant botfly species.

Materials and methods

Study site

The research site was situated in KNR in Xinjiang Province, China (44°40’ to 46°0’ N latitude, 88°33’ to
KNR consists mainly of the Gobi Desert and semi-desert at altitudes of 500–1200 m. It has a typical continental climate with an average annual temperature of 0.2°C (range −49.7 to 45.3°C) and annual precipitation of less than 200 mm, with a 6-month winter [12]. There are four dominant plant species in KNR: Haloxylon ammodendron, Reaumuria soongorica, Ceratoides latens, and Anabasis salsa [33]. There are 21 water sources: 13 permanent and eight seasonal [58]. KNR is one of the few places in the world where the habitats of different wild equids overlap: Przewalski’s horse (Equus ferus przewalskii), the Mongolian wild ass (Equus hemionus hemionus), and domestic horse (Equus ferus caballus) live sympatrically and share pastures seasonally. During the study period, the population of

| Table 1. Frequency distribution of habitat factors in oviposition site selection by G. pecorum in different habitats in KNR. |
|-------------|--------------|--------------|--------------|-------------|-------------------|
| Habitat factor | Category | Qc | Qo | Qt | (Qo/Qt) | n | Σ(Qo/Qt) |
| Altitude (m) | <900 | 1 | 0 | 1 | 0 | 3 | 0.57 |
| 900–1000 | 68 | 91 | 159 | 0.57 | 3 | 0.57 |
| 1000–1100 | 22 | 0 | 22 | 0 | 3 | 0.57 |
| Total vegetation coverage (%) | <10 | 3 | 0 | 3 | 0 | 4 | 1.25 |
| 10–20 | 15 | 5 | 20 | 0.25 | 4 | 1.25 |
| 20–30 | 62 | 73 | 135 | 0.54 | 4 | 1.25 |
| >30 | 10 | 13 | 23 | 0.56 | 4 | 1.25 |
| Stipa capillata coverage (%) | <10 | 5 | 10 | 15 | 0.67 | 4 | 1.634 |
| 10–20 | 18 | 72 | 90 | 0.8 | 4 | 1.63 |
| 20–30 | 52 | 9 | 61 | 0.15 | 4 | 1.63 |
| >30 | 15 | 0 | 15 | 0 | 4 | 1.634 |
| Stipa capillata frequency (%) | <40 | 28 | 19 | 47 | 0.40 | 3 | 1.49 |
| 40–60 | 45 | 50 | 95 | 0.53 | 3 | 1.49 |
| >60 | 17 | 22 | 39 | 0.56 | 3 | 1.49 |
| Stipa capillata height (cm) | <10 | 31 | 26 | 57 | 0.46 | 3 | 1.44 |
| 10–20 | 37 | 50 | 87 | 0.57 | 3 | 1.44 |
| >20 | 22 | 15 | 37 | 0.41 | 3 | 1.44 |
| Ceratoides latens coverage (%) | <5 | 3 | 4 | 7 | 0.57 | 3 | 1.27 |
| 5–10 | 37 | 64 | 101 | 0.63 | 3 | 1.27 |
| >10 | 50 | 23 | 73 | 0.32 | 3 | 1.27 |
| Artemisia sp. coverage (%) | <5 | 13 | 42 | 55 | 0.76 | 3 | 1.39 |
| 5–10 | 49 | 46 | 95 | 0.48 | 3 | 1.39 |
| >10 | 28 | 3 | 31 | 0.097 | 3 | 1.39 |
| Vegetation families | <5 | 78 | 82 | 160 | 0.51 | 3 | 1.29 |
| 5–10 | 10 | 8 | 18 | 0.44 | 3 | 1.29 |
| >10 | 2 | 1 | 3 | 0.33 | 3 | 1.29 |
| Vegetation species | <5 | 79 | 77 | 156 | 0.49 | 3 | 1.34 |
| 5–10 | 9 | 13 | 22 | 0.59 | 3 | 1.34 |
| >10 | 2 | 1 | 3 | 0.33 | 3 | 1.34 |
| Distance to nearest water (m) | <2000 | 70 | 77 | 147 | 0.52 | 3 | 0.92 |
| 2000–5000 | 20 | 14 | 34 | 0.41 | 3 | 0.92 |
| >5000 | 0 | 0 | 0 | 0 | 3 | 0.92 |
| Distance to nearest path (m) | <30 | 65 | 71 | 136 | 0.52 | 3 | 0.92 |
| 30–60 | 13 | 16 | 29 | 0.55 | 3 | 0.92 |
| >60 | 12 | 4 | 16 | 0.25 | 3 | 0.92 |
| Slope direction | S | 13 | 12 | 25 | 0.48 | 4 | 1.91 |
| Sc | 8 | 3 | 11 | 0.27 | 4 | 1.91 |
| S1/2 | 5 | 9 | 14 | 0.64 | 4 | 1.91 |
| Sa | 64 | 67 | 131 | 0.51 | 4 | 1.91 |
| Slope position | P1 | 31 | 29 | 60 | 0.48 | 4 | 2.20 |
| P2 | 6 | 10 | 16 | 0.62 | 4 | 2.20 |
| Pa | 2 | 3 | 5 | 0.6 | 4 | 2.20 |
| Slope gradient (°) | <10 | 70 | 68 | 138 | 0.49 | 4 | 1.48 |
| 10–20 | 15 | 21 | 36 | 0.58 | 4 | 1.48 |
| 20–30 | 3 | 2 | 5 | 0.4 | 4 | 1.48 |
| >30 | 2 | 0 | 2 | 0 | 4 | 1.48 |

Abbreviations: Qc, contrast quadrat; Qo, oviposition site quadrat; Qt, total quadrats; n, eigenvalue; P1, upper position, located in the upper 1/3 of the slope; P2, intermediate position, located in the central part of the slope; Pa, lower position, located in the lower 1/3 of the slope; P0, no slope position; S1/2, semi-sunny, semi-cloudy slope, i.e., N 22.50° ~ E 67.5°, E 22.5° ~ N 67.5° E; Sc, cloudy slope, S67.5° ~ E S22.5° W; Sa, sunny slope, S67.5° ~ E S22.5° W; S, no slope direction.
free-ranging Przewalski’s horses ranged from 86 to 102 horses in six to nine harems and two bachelor groups [58]. Typically, groups of Przewalski’s horses consist of one adult male, several adult females, and their immature offspring, with group sizes of 4–13 individuals [29].

**Habitat observations and Gasterophilus sampling**

We observed two groups of Przewalski’s horses in KNR between March and October 2014. We recorded the location of the groups on a 1:10,000 scale map at 15-min intervals and used the *ad libitum* sampling method [1, 2] to record when the horses entered foraging and resting sites and any behaviours and intergroup encounters. After the wild horses left, we set a 10 × 10 m quadrat as focal quadrat for determining habitat factors when the eggs of *G. pecorum* were found [10, 29]. We also measured the food selection ratio for different food species in the diets of each focal group [29]. A contrast quadrat was placed within about 100 m of the focal quadrat and the same habitat factors were measured. A total of 91 oviposition sites of *G. pecorum* and 90 contrast quadrats were marked on the map. For each oviposition site, we recorded 13 habitat factors (see Table 1 for descriptions and survey methods). For vegetation type, slope gradient, slope direction, slope position, and elevation, the percentage of a particular category within the home range of the horse was considered the availability area.

**Data analysis**

To test for selection or avoidance of a particular category, Ivlev’s electivity index, $E_i$, was calculated as $E_i = (W_i - 1/n)/(W_i + 1/n)$ and $W_i$ was calculated as $W_i = (Q_{O}/Q_{T})\sum (Q_{O}/Q_{T})$, where $E_i$ and $W_i$ are respectively choose coefficient and selection index to measure whether or not species choose a particular habitat. In addition, where $Q_{O}$ is the mean proportion of observations in a particular category, $Q_{T}$ is the mean proportion of this category in the home range, $i$ is the mean characteristic value, and $n$ is the mean eigenvalue of the ecological factors [13, 27, 29]. Then, we used Spearman’s rank correlation to examine correlations between the locations of oviposition sites and the occurrence of seasonal horse behaviour. We used one-way analysis of variance (ANOVA) to test seasonality effects on the usage of oviposition sites. PCA techniques for the identification of common factors in data were used to analyse the main components on adult *Gasterophilus* spp. lay eggs [9]. All data were analysed using SPSS 20.0.

**Results**

**Frequency distribution and selection of habitat factors**

The two horse groups used seasonal and permanent water sources (Fig. 1). The greatest distance from an oviposition site to the nearest water source was <500 m (46/91). Table 2 shows that *G. pecorum* preferred semi-sunny and semi-cloudy slopes, higher and lower slope positions, and slopes of 10–30°. It preferred total plants <10% and *Stipa capillata* coverage <10% in the lower slopes, but *Ceratoides latens* coverage in higher and intermediate slopes. In the lower slope habitat, the numbers of plant species and families was <5. Oviposition sites were often near a water source with a distance <2000 m and average altitude of 900–1000 m. Table 2 presents the frequency distribution of different habitat factors. Most oviposition sites (66/91) were found within 20 m of the nearest path used by equids.

In the principal component analysis of habitat factor on oviposition site quadrats, the main factors were coverage, food, distance, terrain, and altitude (Table 3).

**Discussion**

**Food resources**

The core area around the oviposition site was where the first or last eggs were laid in the habitat. In KNR, more eggs were laid in the core habitat (87 sites) than in the marginal habitat (four sites) [30]. Unlike all previous studies in which *G. intestinalis* was the predominant botfly species, followed by *G. nasalis* (both species have worldwide distributions), these species were the fourth and fifth most common in KNR (Liu, unpublished). This difference might be related to food availability, the surrounding environment, and distribution across habitats.

It is well known that botflies are considered as relatively stenothermal parasites and matured females need warm, sunny, and windless weather. There is no doubt that a higher extensiveness of *Gasterophilus* sp. infection is reported in warmer countries [16, 23, 38, 42]. Moreover, the extensiveness of the infection may be also influenced by the age and sex of examined horses [23]. However, results reported by several authors are not consistent [36, 38, 45]. The climate in northern and central Kazakhstan is continental with hot summers and very cold winters and similar to KNR in China where one finds a typical Gobi Desert habitat, subject to relatively severe climate differences, with a long, cold winter and hot, dry summer [13, 23].

![Figure 1. Location of the Kalamaili Nature Reserve in Xingjiang, China.](image-url)
The KNR area is generally considered to follow non-equilibrium dynamics in biomass production, and as a consequence, ungulate population fluctuations are driven by the amount and timing of rainfall events. G. intestinalis and G. nasalis may not be adapted to this environment. In addition, if the egg shell becomes too dry, the hatching larvae might not be able to exit the shell [53].

G. pecorum female flies lay their eggs on grass and hay [61]. Most of the eggs were laid on S. capillata, which is the main food of equines in KNR. The G. pecorum egg-laying habitat was very similar to the wild horse foraging habitat [29]. Therefore, the botfly behaviour increases the chance that the eggs are eaten by horses and risk of future spread.

### Water resources

Oviposition sites may also be related to water resources [8]. Water is a key resource for most large-bodied mammals in arid environments.

### Table 2. Selective analysis and electivity index of habitat factors in oviposition site selection by G. pecorum in summer in KNR.

| Habitat factor         | Category | Wi  | Ei  | Result |
|------------------------|----------|-----|-----|--------|
| Altitude (m)           | <900     | 0   | -1.0| UC     |
|                        | 900–1000 | 1   | 0.5 | C      |
|                        | 1000–1100| 0   | -1.0| UC     |
| Total vegetation coverage (%) | <10 | 0   | -1.0| UC     |
|                        | 10–20   | 0.2 | 0.3 | C      |
|                        | 20–30   | 0.36| 0.2 | C      |
| Stipa capillata coverage (%) | <10 | 0.10| -0.4| UC     |
|                        | 20–30   | 0.34| 0.2 | C      |
|                        | >30     | 0.32| 0.1 | C      |
| Stipa capillata frequency (%) | <40 | 0.27| -0.1| UC     |
|                        | 40–60   | 0.35| 0.0 | R      |
|                        | >60     | 0.38| 0.1 | C      |
| Stipa capillata height (cm) | <10 | 0.32| 0.0 | R      |
|                        | 10–20   | 0.40| 0.1 | C      |
| Ceratoides latens coverage (%) | <5  | 0.20| -0.3| UC     |
|                        | 5–10    | 0.42| 0.1 | C      |
|                        | >10     | 0.39| 0.1 | C      |
| Artemisia sp. coverage (%) | <5  | 0.53| 0.2 | C      |
|                        | 5–10    | 0.36| 0.0 | R      |
|                        | >10     | 0.11| -0.5| UC     |
| Vegetation families    | <5      | 0.40| 0.1 | C      |
|                        | 5–10    | 0.34| 0.0 | R      |
|                        | >10     | 0.26| -0.1| UC     |
| Vegetation number      | <5      | 0.40| 0.1 | C      |
|                        | 5–10    | 0.23| -0.2| UC     |
|                        | >10     | 0.25| -0.1| UC     |
| Distance to nearest water (m) | <2000 | 0.57| 0.3 | C      |
|                        | 2000–5000| 0.43| 0.1 | C      |
|                        | >5000   | 0   | -1.0| UC     |
| Distance to nearest path (m) | <30 | 0.57| 0.3 | C      |
|                        | 30–60   | 0.60| 0.3 | C      |
|                        | >60     | 0.27| -0.1| UC     |
| Slope direction        | S_D     | 0.25| 0.0 | R      |
|                        | S_C     | 0.14| -0.3| UC     |
|                        | S_U/2   | 0.34| 0.1 | C      |
|                        | S_P     | 0.27| 0.0 | R      |
| Slope position         | P_U     | 0.22| -0.1| UC     |
|                        | P_1     | 0.28| 0.1 | C      |
|                        | P_2     | 0.27| 0.0 | R      |
|                        | P_3     | 0.22| -0.1| UC     |
| Slope gradient (°)     | <10     | 0.33| 0.1 | C      |
|                        | 10–20   | 0.40| 0.2 | C      |
|                        | 20–30   | 0.27| 0.0 | R      |
|                        | >30     | 0   | -1.0| UC     |

Abbreviations: UC, not chosen; C, chosen; R, random; other abbreviations as in Table 1.
Wang and Xu [56] and Pilo et al. [41] confirmed that female eggs on grass and hay [61]. In agreement with previous studies, vegetation families covered different plant species. Table 3 shows the PCA variable loadings and factors associated with oviposition site selection. The factors include altitude, vegetation cover, distance to water, slope, and vegetation number. We found that female G. pecorum lay their eggs on S. capillata in KNR and with about 2–4 eggs adhered to each plant. This egg scattering behaviour is advantageous for infecting the host. Chereshnev [11] reported that roughly 1300–2400 G. pecorum eggs can infest an entire ranch. The trend of oviposition of different Gasterophilus spp. (other than G. pecorum) is to lay eggs at different sites of the horse’s coat [41] that match the wild horse habitat, which may be an adaptive behaviour in the co-evolution of host (horse) and parasite (Gasterophilus). This behaviour of G. pecorum provides better opportunities for success in infesting a suitable host after hatching, and reduces the chance of offspring dying for lack of a host [39]. Asiatic wild asses are potentially exposed to a higher risk of parasite re-infection due to their temporal aggregation in very large groups.

### Other factors related to oviposition site selection

Female G. intestinalis deposit their eggs mainly on the distal forelegs of the host and occasionally on the hindlegs and belly. Females of G. nasalis, G. haemorrhoidalis, G. inermis, and G. nigricornis deposit their eggs on the head, near the mouth. Unlike the other species, female G. pecorum lay their eggs on grass and hay [61]. In agreement with previous studies, Wang and Xu [56] and Pilo et al. [41] confirmed that female G. pecorum lay their eggs in pasture. By contrast, Cogley and Cogley [14] reported that G. intestinalis female flies lay eggs on the coat of horses. Coat colour also would seem to influence the number of eggs laid and adult flies have been shown to prefer darker horses and nearly ignored the lighter horse that was grazing in the immediate vicinity, whereas according to Pandey et al. [40] and Brocard and Pfister [7] there is no preference or attraction by Gasterophilus flies to any particular colour of horse.

We found that female G. pecorum laid their eggs on S. capillata in KNR and with about 2–4 eggs adhered to each plant. This egg scattering behaviour is advantageous for infecting the host. Chereshnev [11] reported that roughly 1300–2400 G. pecorum eggs can infest an entire ranch. The trend of oviposition of different Gasterophilus spp. (other than G. pecorum) is to lay eggs at different sites of the horse’s coat [41] that match the wild horse habitat, which may be an adaptive behaviour in the co-evolution of host (horse) and parasite (Gasterophilus). This behaviour of G. pecorum provides better opportunities for success in infesting a suitable host after hatching, and reduces the chance of offspring dying for lack of a host [39]. Asiatic wild asses are potentially exposed to a higher risk of parasite re-infection due to their temporal aggregation in very large groups.

### Synthesis and applications

It is important to study how and why eggs are distributed across potential hosts by ovipositing females. Such studies have historically been dominated by the “preference-performance problem” [32, 50], under the assumption that host preference has evolved to assure maximum offspring performance. An ovipositing female is faced with some intricate problems. She has to process sufficient information to locate and evaluate potential locations for oviposition, and to select problems. She has to process sufficient information to locate and evaluate potential locations for oviposition, and to select suitable oviposition sites based on her performance constraints. This is in itself a complex, resource-intensive task, especially when the range of possible oviposition locations or prey types increases [3, 17]. This hypothesis appears to be verified by G. pecorum, because the flies choose only S. capillata for laying eggs among numerous plant species.
References

1. Altmann J. 1974. Observational study of behavior, sampling methods. Behaviour, 49, 227–262.
2. Altmann SA. 1974. Baboons, space, time and energy. American Zoologist, 14, 221–248.
3. Bernays EA. 2001. Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. Annual Review of Entomology, 46, 703–727.
4. Bolger DT, Newmark WD, Morrison TA, Doak DF. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters, 11, 63–77.
5. Bouman I. 2006. The Tale of the Przewalski’s Horse. KNNV Publishers: Utrecht, The Netherlands. p. 82–161.
6. Brandt M, Fischer B, Heinze J, Foitzik S. 2007. Population structure and the co-evolution between social parasites and their hosts. Molecular Ecology, 16, 2063–2078.
7. Brocard P, Pfister K. 1991. The epidemiology of Gasterophilosis of horses in Switzerland. Schweizer Archiv für Tierheilkunde, 133, 409–416.
8. Chapman RF, SJ Simpson, AE Douglas. 2012. The insects: structure and function, 5th edn. Elsevier North Holland, Inc: New York. p. 543–635.
9. Charles D. 1998. Constrained PCA techniques for the identifi- cation of common factors in data. Neurocomputing, 22, 145–156.
10. Chen JL. 2008. Utilization of food, water and space by released Przewalski horse (Equus przewalski) with reference to survival strategies analysis. Beijing Forestry University: Beijing, China.
11. Chereshevn NA. 1951. Biological peculiarities of the botfly Gasterophilus pectorum Fabr. (Diptera: Gasterophilidae). Doklady Akademii Nauk SSSR, 77, 765–768 (in Russian).
12. Chu HJ. 2008. The feeding, population and habitat research between (Equus hemionus) and geese antelope (Gazella subgutturosa) in Kalamaili wild ungulates nature reserve. Chinese Academy of Sciences University: Beijing, China.
13. Chu HJ, Jiang ZG, Ge Y, Jiang F, Tao YS, Wang C. 2009. Population densities and number of khulan and goitered gazelle in Mt. Kalamaili Ungulate Nature Reserve. Biodiversity Science, 17, 414–422.
14. Cogley TP, Cogley MC. 2000. Field observations of the host-parasite relationship associated with the common horse bot fly, Gasterophilus intestinalis. Veterinary Parasitology, 88, 93–105.
15. Colwell DD, Hall MJR, Scholl PJ. 2006. The oestrid flies: biology, host-parasite relationships, impact and management. Oxford University Press: London.
16. Drudge JH, Lyons ET, Wyatt ZN, Tolliver SC. 1975. Occurrence of second and third instars of Gasterophilus intestinalis and Gasterophilus nasalis in stomachs of horses in Kentucky. American Journal of Veterinary Research, 36, 1585–1588.
17. Dukas R. 2002. Behavioral and ecological consequences of limited attention. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 357, 1539–1547.
18. Fryxell JM, Sinclair ARE. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution, 3, 237–241.
19. Gandon S, Michalakis Y. 2002. Local adaptation, evolutionary potential and host-parasite coevolution: interactions between migration, mutation, population size and generation time. Journal of Evolutionary Biology, 15, 451–462.
20. Gaylard A, Owen-smith N, Redfern J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes, in The Kruger Experience: Ecology and Management of Savanna Heterogeneity, du Toit JT, Rogers KH, Biggs HC, Editors. Island Press: Washington, DC, USA. p. 171–188.
21. Hagemone RIM, Reimer E. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology, 71, 883–892.
22. Hummel J, Steuer P, Südekum KH, Hammer S, Hammer C, Streich WJ, Clauss M. 2007. Fluid and particle retention in the digestive tract of the addax antelope (Addax nasomaculatus) – adaptations of a grazing desert ruminant. Comparative Biochemistry and Physiology – Part A, Molecular & Integrative Physiology, 149, 142–149.
23. Ibrayeva B, Lidera L, Christian B. 2015. Gasterophilus spp. infections in horses from northern and central Kazakhstan. Veterinary Parasitology, 207, 94–98.
24. Kaczensky P, Ganbaatar O, Von-Wehrden H, Walzer C. 2008. Resource selection by sympatric wild equids in the Mongolian Gobi. Journal of Applied Ecology, 45, 1762–1769.
25. Kaczensky P, Ganbaatar O, Weihrden HV, Enksaikhn N, Lkhagvasuren D, Walzer C. 2007. Przewalski horses reintroduction in the great Gobi B strictly protected area from species to ecosystem conservation. Mongolia Journal Biological Sciences, 5, 13–18.
26. King SRB, Gurnell J. 2010. Effects of fly disturbance on the behaviour of a population of reintroduced Przewalski horses (Equus ferus przewalskii) in Mongolia. Applied Animal Behaviour Science, 125, 22–29.
27. Lechowicz MJ. 1982. The sampling characteristics of electivity indices. Oecologia, 52, 22–30.
28. Li K, Wu Z, Hu DF. 2007. A report on new causative agent (Gasterophilus spp.) of the myiasis of Przewalski’s horse occurred in China. Chinese Journal of Animal and Veterinary Sciences, 38(8), 837–840.
29. Liu S. 2013. Study on habitat selection and community protection awareness of the reintroduced Equus przewalskii in Mt. Kalamaili Ungulate Nature Reserve. Xinjiang University: Xinjiang, China.
30. Liu SH. 2012. Morphology and epidemiological investigation and the mitochondrial Cytochrome Oxidase I (COI) and 16S rRNA gene phylogenetic of Gasterophilus. Beijing Forestry University: Beijing, China.
31. Lozano GA. 1991. Optimal foraging theory: a possible role for parasites. Oikos, 60, 391–395.
32. Mayhew PJ. 2001. Herbivore host choice and optimal bad motherhood. Trends in Ecological Evolution, 16, 165–167.
33. Meng YP. 2007. Studies on the food plants, food preference and foraging strategy of released Przewalski’s horses. Beijing Forestry University: Beijing, China.
34. Mo F. 2010. The Gasterophilus myiasis research of Przewalski’s horses (Equus przewalskii). Beijing Forestry University: Beijing, China.
35. Mohr E. 1971. The Asiatic wild horse. Allen: London.
36. Niedzwiedz A, Borowicz H, Nicpon JM. 2013. Prevalence study in horses infected by Gasterophilus sp. in an eastern region of Poland. Veterinary Parasitology, 191, 94–96.
37. Ostrowski S, Williams JB, Ismael K. 2003. Heterothermy and the water economy of free-living Arabian oryx (Oryx leucoryx). Journal of Experimental Biology, 206, 1471–1478.
38. Otranto D, Milillo P, Capelli G, Colwell DD. 2005. Species nematode parasitism and its significance in parasitism. Advances Veterinary, 78, 43–52.
39. Pandey VS, Ouhelli H, Elkhalfane A. 1980. Observations on the epizootiology of Gasterophilus intestinalis and G. nasalis in horses. Veterinary Parasitology, 7, 347–356.
40. Pilo C, Altea A, Fois MP, Scala A. 2009. Equine Gasterophi-losis in Sardinia: annual trend of bot eggs laying in different topographic regions of the horse. Veterinary Research Communications, 33, 149–151.
41. Principato M. 1989. Observations on the occurrence of five species of Gasterophilus larvae in free-ranging horses in Umbria, central Italy. Veterinary Parasitology, 31, 173–177.
42. Principato M. 1988. Classification of the main macroscopic lesions produced by larvae of Gasterophilus sp. (Diptera: Gasterophilidae) in free-ranging horses in Umbria. Cornell Veterinary, 78, 43–52.
43. Rogers WP. 1963. The infective stage of nematode parasites and its significance in parasitism. Advances in Parasitology, 1, 109–178.
44. Romanuk K, Snarska A. 2002. Existence of horse botfly Gasterophilus intestinalis eggs on coats of mares, suckling colts and young mares and colt of primitive Polish horses. Medycyna Veterynaryjna, 2002(58), 641–643.
45. Salz D, Rowen M, Rubenstein DI. 2000. The impact of space use patterns of reintroduced Asiatic wild ass on effective population size. Conservation Biology, 14, 1852–1862.
46. Sandin A, Skidell J, Haggstrom J, Girma K, Nilsson G. 1999. Post-mortem findings of gastric ulcers in Swedish horses up to one year of age: a retrospective study 1924–1996. Acta Veterinaria Scandinavica, 40, 109–120.
47. Sarah R, King B, Gurnell J. 2010. Effects of fly disturbance on the behaviour of a population of reintroduced Przewalski horses (Equus ferus przewalskii) in Mongolia. Applied Animal Behaviour Science, 125, 22–29.
48. Scheibe KM, Eichhorn K, Kalz B, Streich WJ, Scheibe A. 1998. Water consumption and watering behavior of przewalski horses (Equus ferus przewalskii) in a semireserve. Zoo Biology, 17, 181–192.
49. Scheirs J, De Bruyn L. 2002. Integrating optimal foraging and optimal oviposition theory in plant-pest insect research. Oikos, 96, 187–191.
50. Sequeira JL, Tostes RA, Oliveira-Sequeira TC. 2001. Prevalence and macro- and microscopic lesions produced by Gasterophilus nasalis (Diptera: Oestridae) in the Botucatu Region, SP, Brazil. Veterinary Parasitology, 102, 261–266.
51. Sievers G, Weber B. 2005. Egg laying period of Gasterophilus nasalis and G. intestinalis on horses. 8th Region, Chile. Archivos de Medicina Veterinaria, 37, 169–172.
52. Studzinska MB, Wojcieszak K. 2009. Gasterophilus sp. botfly larvae in horses from the south-eastern part of Poland. Bulletin of the Veterinary Institute in Pulawy, 53, 651–655.
53. Swingland IR, Greenwood PJ. 1983. The ecology of animal movement. Clarendon: Oxford.
54. Taylor MA, Coop RL, Wall RL. 2007. Veterinary Parasitology, 3rd edn. Blackwell Publishing, UK.
55. Wang SZ, Xu XZ. 1991. The geographical distribution of Gasterophilus in Xinjiang, China. Journal of Veterinary Science and Technology, 21, 14–16.
56. Wang WT, Zhang D, Hu DF, Chu HH, Cao J, Ente M, Li K. 2014. Population genetic structure of Gasterophilus pecorum in the Kalamaili Nature Reserve, Xinjiang, based on mitochondrial cytochrome oxidase (COI) gene sequence. Medical and Veterinary Entomology, 28, 75–82.
57. Wang Y. 2014. Study on habitats, populations and home ranges of the reintroduced Przewalski’s horses and activities rhythms of coexistence wolves. Xinjiang University: Xinjiang, China.
58. Xiang C, Cao J, Zhang H, Gao X, Yang W, Blank D. 2014. Reintroduction of Przewalski’s horse (Equus ferus przewalskii) in Xinjiang, China: the status and experience. Biological Conservation, 177, 142–147.
59. Zaheri BA, Ronaghi H, Youseffi MR, Hoseini SM, Omidzahir S, Dozouri R, Eshkevari SR, Mousapour A. 2014. Gasterophilus pecorum and Habronema muscae in Persian onager (Equus hemionus onager), histopathology and parasitology survey. Journal of Comparative Clinical Pathology, 24, 1009–1013.
60. Zumpt F. 1965. Myiasis in man and animals in the old world. Butterworths: London. p. 110–129.
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