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Epidemiology and risk factors for endoparasite infection in subtropical feral cattle in Hong Kong

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ABSTRACT

Understanding parasite epidemiology is essential for managing endoparasite infections in free-ranging animals. However, such epidemiological knowledge is limited for feral cattle and is usually derived from farmed populations. We assessed endoparasite infection in a feral cattle population in Hong Kong. This population does not receive any routine care or anthelmintic treatment, although some cattle are provisioned with water and hay by local citizens. We assessed three indices of endoparasite infection (parasite richness, prevalence and fecal egg/oocyst count) and their associated risk factors (season, provisioning, marshland access, group size, sex and body condition) in adult cattle.

We conducted sedimentation, McMaster and coproculture techniques on 262 samples collected from 177 cattle. We identified eleven taxa of nematodes, two taxa of trematodes, one taxon of protozoan and one taxon of cestode. Median parasite richness was two parasite taxa per individual. Trematode infections were the most prevalent (91.22 %), followed by protozoan (67.17 %), nematode (23.22 %) and cestode (12.97 %) infections. Counts averaged 144.85 oocysts per gram for *Eimeria* oocysts, 20.61 eggs per gram (EPG) for strongyle-type eggs, 11.83 EPG for *Moniezia* and 1.91 EPG for *Trichostrongylus*. Provisioned herds were more likely to be infected with *Eimeria*, but had lower prevalence of *Trichostrongylus*. *Eimeria* prevalence and strongyle-type egg counts were higher in the wet season, while *Fasciola* eggs, *Cooperia* and *Trichostrongylus* larvae were more prevalent in the dry season. Larger herds had higher *Eimeria* oocyst prevalence but lower *Fasciola* egg prevalence. Marshland access decreased *Fasciola* egg prevalence while it increased prevalence of *Cooperia* larvae. Males were more infected with strongyle-type eggs than female cattle.

We show that the seasonal dynamics of infection and consequences of provisioning differ between endoparasite taxa. Our findings highlight complex interactions between endoparasites and their hosts, providing new insights into wild ruminants' health and the impacts of anthropogenic provisioning.

1. Introduction

In wild tropical and subtropical ruminant populations, knowledge of endoparasite infections has focused on African fauna (Ezenwa and

Worsley-Tonks, 2018; Ezenwa, 2003), with less known about Asian wild ruminants. For domestic ruminants returned to natural settings (*i.e.*, feral), knowledge of endoparasites is usually generalized from farmed or wild populations, with few studies specifically addressing this topic (*e.g.*,

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Thapa et al., 2022). The main endoparasites infecting ruminants are protozoa, cestodes, trematodes and nematodes (Loginova et al., 2023; Patra et al., 2022) and co-infections with these are the norm (Cattadori et al., 2008; Thumbi et al., 2014). Many endoparasite infections in ruminants are subclinical with few to no clinical signs (Koltz et al., 2022). However, endoparasites can increase mortality and cause population decline in wild ruminants (MacPhee and Greenwood, 2013; Thompson, 2013), altering population dynamics which can detrimentally affect ecosystem biodiversity and stability (Sánchez et al., 2018; Thompson et al., 2010). In addition, wild animals may act as a source of infection for domesticated animals or zoonotic infections for people (Colston and Mearns, 2023; Thompson, 2013). Wild populations can also become infected due to their proximity to human settlements and domestic livestock (Allwin, 2015). Understanding parasite epidemiology is critical for managing endoparasite infection in such populations.

Variation in individual infection risk, defined as the probability that an individual host acquires an infection, is reflected in population level infection patterns (Akinyi et al., 2019). Host exposure and susceptibility contribute to this variability (Sweeny and Albery, 2022). Exposure is the likelihood that an individual host will encounter infectious material, while susceptibility refers to the likelihood of an individual developing an infection upon contact with infectious material (Müller-Klein et al., 2019). Risk factors are variables that impact individual infection risk, at both exposure and susceptibility levels. In ruminants, the main risk factors for endoparasite infections are related to ecological (e.g., climate, weather, land type, population density, food availability, group size and production system) and biological (e.g., age, sex, reproductive status, body condition, nutritional state and immunocompetency) factors (Kołodziej-Sobocińska, 2019). The role of anthropogenic factors, notably provisioning in wild populations of ungulates, has also been extensively studied in temperate systems (Milner et al., 2014; Murray et al., 2016), although information is lacking in tropical and subtropical populations. In wild and feral populations, the evaluation of risk factors is limited by feasibly obtainable data.

While cattle (*Bos taurus*) are estimated to be the second main contributor to mammal biomass after humans (Greenspoon et al., 2023) with about 1.5 billion cattle worldwide (FAO, 2021), research primarily focuses on farmed livestock. There are very few remaining feral populations (e.g., Berteaux and Micol, 1992; Hall et al., 2021; Thapa et al., 2022), and no wild cattle (*Bos primigenius*) population has existed since the 16th century (Van Vuure, 2002; Vuković, 2021). There is a notable research bias towards cattle in temperate areas and production systems. In subtropical livestock systems, endoparasite infections occur frequently in cattle, in particular protozoan infections (e.g., Taiwan: Huang et al., 2014; Tung et al., 2012; Vietnam: Geurden et al., 2008). In these systems, several risk factors have been identified, with males having higher infection rates of the protozoan *Eimeria* than females (Singh et al., 2012) and marked seasonal variation in infection risk (Rahman et al., 2012). Further understanding can be drawn from closely related bovids in subtropical areas. For instance, research into endoparasites of Gaur (*Bos gaurus*) highlights co-occurring infections with protozoa, cestodes, trematodes and nematodes (Allwin, 2015). Similarly, banteng (*Bos javanicus*) are infected with a wide range of endoparasites, most of which are shared with nearby cattle, further highlighting similarities between wild and domestic bovids (Watwiengkam et al., 2024). Nepalese feral cattle were found to carry high infection rates of endoparasites (72 %) but low counts of eggs and oocysts were found in fecal samples, with no sex differences (Thapa et al., 2022). Understanding epidemiology of endoparasites in subtropical climates and identifying risk factors is essential to enhance our knowledge of bovid adaptations to parasite pressures and to ensure efficient and appropriately targeted interventions.

The Hong Kong (HK) feral cattle are unique in their genetic profile and origin; a cross-breed of *Bos taurus taurus* and *Bos taurus indicus* that share genetic similarities with South Asian wild bovids (Barbato et al., 2020). These cattle were used as draught animals until they were

released to the wild when agricultural activities declined in HK during the 1950s–1970s. No veterinary care or anthelmintic treatments were documented before their release, with parasite control relying on elimination of intermediate hosts and treatment of humans at risk of transmission (Cockrill, 1976). Nowadays, the HK feral cattle are regarded as part of the local heritage and have been characterized as both wild and feral (Pei et al., 2010; Zhang, 2025). Knowledge on their behavior, ecology and welfare is limited (Hodgson et al., 2024; LegCo, 2017; Pinkham et al., 2022; So and Dudgeon, 2020). The cattle have year-round access to water bodies, although seasonal variations (e.g., rainfall and flooding events) influence water availability. Some herds are provisioned with commercial hay, fresh-cut grass and tap water from local citizen groups. The HK feral cattle are overseen by the Agriculture, Fisheries and Conservation Department (AFCD) of the Government of the Hong Kong Special Administrative Region (HKSAR) (AFCD, 2018), who provide emergency treatment only when indicated, on an individual welfare basis.

Currently, no data on endoparasites in HK feral cattle are available. Investigating endoparasite richness (number of parasite taxa present per sample), prevalence (presence/absence of each parasite taxon in each sample), and count (number of eggs/oocysts for each taxon found in each sample) in this unique population is a rare opportunity to observe parasitism in cattle in the absence of anthelmintic treatments or management interventions. Our study was conducted to identify the epidemiology of endoparasites in HK feral cattle using non-invasive sampling. Based on previous knowledge in wild and feral subtropical bovids and farmed cattle, we expected to find protozoa, cestodes, trematodes and nematodes. We expected endoparasites to be impacted by ecological and biological risk factors. Constrained by our knowledge in this population, we evaluated the associations between endoparasite infection and season, provisioning, water body access, group size, sex and body condition. Specifically, we expected all parasite measures (richness, prevalence and count) to be higher in the wet season than in the dry season. Provisioned herds were expected to display higher prevalence of nematodes due to accumulation of infective material near feeding areas, while no differences were expected for other parasites. Access to marshlands was expected to increase rates of trematode infection due to the necessity of such areas for intermediate trematode hosts, and hence for trematodes to develop to stages able to infect cattle. We also expected larger herds to have higher richness, prevalence, egg counts and oocyst counts than smaller herds. We expected males and individuals with lower body condition to display higher measures of parasite infections.

2. Material & methods

Ethical approval

This research was reviewed and approved by the Animal Research Ethics Sub-Committee of City University of Hong Kong (approval number A-0826). Sampling was non-invasive, observational, purely opportunistic, and conducted in the cattle's natural environment.

2.1. Study site and cattle

Cattle were located across three country parks in New Territories, HK (Fig. S1): Sai Kung East Country Park (22.4085°N, 114.3435°E), Plover Cove Country Park (22.5206°N, 114.2447°E) and Tai Lam Country Park (22.3939°N, 114.0067°E). We had existing information on these herds, including herd location and demographics, based on other ongoing long-term projects requiring frequent visits to the cattle including between the samplings of the present study. These cattle graze and browse on grasslands, marshlands and forests. Animal identification was based on ear tags (previously applied by the AFCD, 41 % of cattle in the study sample were tagged), a photo-based catalogue and phenotypic descriptive indices.

Our study was conducted from December 2022 to February 2023 for the dry season, and from July to August 2023 for the wet season. We sampled 141 individual cattle (males = 61, females = 80) from seven herds in the dry season, and 121 individuals (males = 54, females = 67) from six herds in the wet season. Eighty-five individuals were sampled in both seasons, 56 were sampled only in the dry season, and 36 only in the wet season. In total, 262 samples were collected. Key characteristics of each herd are further described in [Table S1](#) (e.g., provisioning status, herd size, sex ratio).

2.2. Risk factor identification

Based on literature, we identified six known risk factors related to endoparasitism in ungulates that were applicable to our feral cattle population ([Table S2](#)). These were season ([Cizauskas et al., 2015](#); [Sun et al., 2018](#)), provisioning ([Hines et al., 2007](#); [Navarro-Gonzalez et al., 2013](#)), access to water bodies ([Titcomb et al., 2021](#)), group size ([Ezenwa and Worsley-Tonks, 2018](#)), sex ([Kaewthamasorn and Wongsamee, 2006](#); [Thapa et al., 2022](#); [Turner et al., 2012](#)) and body condition ([Aragaw and Tilahun, 2019](#); [Dorny et al., 2011](#); [El-Tahawy et al., 2017](#); [Kaewthamasorn and Wongsamee, 2006](#); [Turner et al., 2012](#)).

Although reproductive status is an important risk factor for a wide variety of endoparasite taxa infections ([Cizauskas et al., 2015](#); [Turner et al., 2012](#)), we were unable to assess this within our context. The AFCD aims to achieve a stable feral cattle population minimizing potential for human-cattle conflict ([AFCD, 2018](#)), and performs reproductive control via surgical sterilization and immunocontraception of some individuals within the population. It is estimated that about 62 % of males are sterilized with female sterilization also occurring ([Pinkham et al., 2022](#)), but individual reproductive status is unknown and so could not be considered in our analyses.

Similarly, although age is a risk factor for endoparasite infection in cattle, with juveniles being more susceptible to a wide variety of infections ([Aragaw and Tilahun, 2019](#); [El-Tahawy et al., 2017](#)), the low number of juveniles in the sampled population (only five calving events occurred during our sampling period across of all seven herds) meant we were unable to reach a valid sample size for younger animals. Therefore, we only sampled adult cattle. Within adult cattle, age estimation was not possible, as the common methods for age estimation could not be used. Examination of teeth ([Jones and Sadler, 2012](#); [Mushonga et al., 2020](#)) and body size measurements ([Masho et al., 2022](#)) for age estimation was not possible due to inability to restrain cattle. Additionally, HK cattle have very little variation in body size and estimation of age based on horn length was also inapplicable as 22 % of females and 11 % of males have broken horns ([Perroux et al., 2025](#)). While some individuals in our population are estimated to be older than 13 years old ([LegCo, 2017](#)), such estimates are not available for most individuals. We therefore limited our data collection to adult cattle and did not attempt to estimate individual age.

Three of the seven herds were provisioned with commercial hay, fresh cut grass and tap water from local citizen groups on a variable basis ([Table S1](#)), although the exact amount provided was unknown. Although no systematic scoring was conducted, during data collection we observed that provisioned herds tended to spend more time in the same area, independent of the presence of people feeding them (i.e., remained nearby even in days they were not provisioned), while non-provisioned herds appeared to range more. This is consistent with previous observations in wild/free-ranging populations ([Becker et al., 2015](#); [Murray et al., 2016](#)).

As all herds had free access to natural water sources such as streams and reservoirs, water body access was quantified based on cattle access to marshlands (as a binary variable yes/no), using our direct observations during fieldwork ([Table S1](#)). Marshlands were defined using the following criteria: freshwater, unmanaged and with a minimum size of 5 m² ([Ades et al., 2013](#); [Dudgeon and Chan, 1996](#)).

Group size was measured as the total number of individuals observed

in a herd over the collection period. Individuals that changed herd over the study period were included in the group size count of two herds, this was the case for four individuals (one female and three males). Group size ranged from 18 to 65 individuals ([Table S1](#)).

Each individual received a Body Condition Score (BCS) at the time of each fecal sampling based on a modified visual 9-point scale, with 1 being the thinnest individuals (low body condition), and 9 the fattest (high body condition). This scale was adapted to the HK feral cattle based on beef and dairy cattle BCS ([D'Occhio et al., 2019](#); [Weik et al., 2021](#)). To control for the subjective nature of body condition scoring, training was conducted to ensure good scorer reliability (for six weeks from April 1st 2022 to May 5th 2022), with body condition scored once a week by a single observer on all cattle in a single herd (n = 65). BCS scores were expected to be highly correlated from one week to the subsequent week, therefore the scorer trained until BCS from one week to the subsequent reached a significant correlation of more than 0.8 for three consecutive weeks. This same observer scored all BCS used in the present study on endoparasites.

2.3. Fecal collection

During the wet and dry season samplings, we tracked all herds on foot for a maximum of 4 h each sampling day and stood at a minimum of 10 m away from the cattle. When individuals were observed defecating, 20–30g of freshly voided fecal material was collected from the ground after the cattle stepped away, and samples were placed into resealable polythene bags labelled with the animal's identification. Two samples were collected for each individual, one was stored immediately in a cooler bag at 4 °C, while the other was stored at ambient environmental temperature for transport to the CityU Veterinary Diagnostic Laboratory at City University of Hong Kong.

2.4. Parasitological analysis

Fecal samples stored at 4 °C during transport were used for McMaster and sedimentation techniques ([Hansen and Perry, 1994](#)). The McMaster technique is a flotation procedure for determining the fecal egg count (FEC) and fecal oocyst count (FOC) of distinguishable nematode eggs, cestode eggs and protozoan oocysts. FECA-MED (fecal medium) 35.6 % (w/w) sodium nitrate fecal flotation solution with specific gravity of 1.25–1.30 was used (VEDCO Inc., St. Joseph, Missouri, USA). 2g of feces from each sample were mixed with 28 ml of flotation solution and loaded into a McMaster slide chamber, as recommended by [Pasquini and Pasquini \(2004\)](#). With reference to 'The RVC/FAO Guide on Veterinary Diagnostic Parasitology' ([Gibbons et al., 2022](#)), microscopic identification of parasite species in each fecal sample was based on morphological characteristics of the oocysts or eggs under 100x magnification on a light microscope, allowing calculation of egg counts expressed in eggs per gram (EPG) and oocyst counts expressed in oocyst per gram (OPG), with a 50 EPG/OPG sensitivity. As fecal flotation solutions are unsuitable for trematode eggs due to their larger size and heavier weight, we used a fecal sedimentation technique. For this, 1g of feces from each sample was mixed with 10 ml of tap water creating a fecal/water suspension. The supernatant was discarded, and the sediment was stained with one drop of methylene blue solution, enabling identification to generic level under 100x or 400x magnification on a light microscope for *Fasciola* and Paramphistomid eggs.

Fecal samples transported at ambient environmental temperature were used for larval culture. As strongyle-type nematode eggs are indistinguishable up to genus level, samples in which strongyle-type eggs were detected using the McMaster technique were then cultured to allow development of the L3 stage ([Hansen and Perry, 1994](#)). 20g of each fecal sample was loaded into a glass jar and incubated at 27 °C for 7–10 days. This variation in incubation time was due to schedule constraints (time required for sample processing, as well as laboratory closure days following major weather events such as typhoons and

flooding). Then, we used a modified Baermann technique to extract the larvae, where 10g of each cultured sample were suspended in distilled water for 24 h to allow for sedimentation of larvae. The larval sediment was extracted with a pipette onto a microscope slide and was stained with one drop of Lugol's iodine solution. Recovered larvae were then identified under a light microscope at 100x and 400x magnification based on their morphological identification keys. Specifically, we used (i) overall larval length, (ii) larval tail presence and length, (iii) filament presence and proportion, (iv) presence of sheath, (v) shape of larval head, (vi) number of intestinal cells and (vii) presence of refractile bodies to identify larvae at genus level as recommended by Van Wyk and Mayhew (2013). These measurements were performed using microscopic pictures obtained with the software Labscope (Zeiss, 2024, version 4.2). This allowed identification of *Bunostomum*, *Chabertia*, *Cooperia*, *Dictyocaulus*, *Haemonchus*, *Oesophagostomum*, *Ostertagia* and *Trichostrongylus* larvae. While *Dictyocaulus* does not require an incubation period, our coproculture provided the necessary conditions for its maintenance and Baermann is a suitable technique for its detection (Cezaro et al., 2018; Verocai et al., 2020).

Endoparasite infections were defined along three measures: parasite richness, defined as the number of parasite taxa documented in infected individuals; parasite prevalence, defined as the proportion of individuals in our sample for which each taxa's eggs/oocysts were detected in feces; and parasite egg/oocyst counts, defined as the number of each taxon's eggs/oocysts per gram of feces in each sample (Griffin and Nunn, 2012; Shaw et al., 2018; Turner and Getz, 2010). Parasite counts could only be obtained for nematodes (strongyle-type and *Trichuris*), cestodes (*Moniezia*) and protozoa (*Eimeria*), using fecal and oocyst egg count (FEC and FOC) from the McMaster technique, where for each sample, the number of eggs/oocysts counted in the slide chambers were added together then multiplied by 50 (Hansen and Perry, 1994; Pasquini and Pasquini, 2004). Parasite counts are presented as mean \pm standard deviation. We could not calculate trematode count, as the sedimentation technique we selected is a qualitative rather than quantitative technique. Additionally, as we did not do a differential count based on larval identification, counts are only available at the ordinal level for strongyle-type eggs and reflect the counts of combined genera of strongylids producing indistinguishable eggs.

2.5. Statistical analysis

All statistical analyses were conducted with R (R Core Team, 2020; version 4.3.3) with datasets and scripts provided on the OSF online platform (Perroux et al., 2023). For prevalence (presence/absence of each parasite taxon per sample), taxon prevalences with low variance (below 0.1) were excluded from further analysis due to lower occurrence of egg/oocyst detection than acceptable given our sample size (Hsieh et al., 1998). Similarly, only parasite taxon whose counts had more than 20 % of data containing non-zero values were further analyzed. While there is no critical number of zero values previously defined (Fox et al., 2015; Zuur and Ieno, 2016), we made this decision in view of our context and methodology, with zero counts likely containing a mix of true (samples containing no eggs/oocysts) and false zeros (samples containing less eggs/oocysts than our sensitivity threshold of 50 and therefore detected as 0).

Risk factors for endoparasite infection were analyzed using generalized linear mixed models with varying distributions depending on the nature of the outcome variable. A Poisson distribution, a Bernoulli distribution and a zero-inflated negative binomial distribution were specified for richness, prevalences and counts, respectively (Zuur and Ieno, 2016). Package "glmmTMB" (Brooks et al., 2017) was used to fit the aforementioned models with herd being forced into the model as a random effect. We developed the multivariable model using a backwards elimination approach to quantify the effects of the risk factors (Heinze et al., 2018; Ullmann et al., 2024). Initially, all candidate independent variables were included (Table S3), and we used the

likelihood ratio test (LRT) to assess whether each of the variables was associated with the outcome. Variables with the highest p-values were removed stepwise until only significant variables remained. To account for confounding, we examined whether excluding a variable changed the regression coefficients or standard errors of other variables by more than 15 % (Table S4). Any confounding variable was forced in the model, regardless of its p-value. After finalizing the variable selection, we tested for the interaction between sex and body condition, as well as the interaction between provisioning and body condition score, since they were deemed biologically plausible based on previous research in wild ungulates (Bostal et al., 2024; Hewison et al., 2024; McElligott et al., 2003). Significant interactions were included if they improved model fit, as assessed by the LRT. This procedure resulted in different variables selected in each model, further presented in Table S5. Model assumptions were examined based on guidelines provided by Zuur and Ieno (2016).

The effects of a risk factor on infection indices are presented as risk ratios or odd ratios (for prevalence data) and their corresponding 95 % confidence intervals (95 %CI). For zero-inflated models, outputs are presented using both: (i) the statistical count output in terms of likelihood or not of being infected; and (ii) in terms of egg/oocyst counts to compare parasite counts between risk factors. For this reason, although models of *Eimeria* prevalence and output (i) from the zero-inflated *Eimeria* oocyst counts model provide similar information, the zero-inflated output (ii) differs, justifying the presence of both models. Similarly, as the prevalence of *Trichostrongylus* was much higher than other strongyle-type nematodes, our zero-inflated strongyle-type egg count model output (i) may provide information that overlaps with our model for *Trichostrongylus* prevalence. As we do not have differential counts at generic level for this order, we are unable to investigate this further.

3. Results

3.1. Descriptive statistics for endoparasite infection in HK feral cattle

Fifteen taxa of endoparasites were identified, comprising eleven taxa of nematodes, two taxa of trematodes, one taxon of protozoa and one taxon of cestodes (Table 1). Trematode infections were the most prevalent (91.22 %, 95 %CI = 87.17–94.07), followed by protozoan (67.17 %, 95 %CI = 61.27–72.57), nematode (23.66 %, 95 %CI = 18.92–29.16) and cestode (12.97 %, 95 %CI = 9.43–17.58) infections. Paramphistomid eggs were the most prevalent trematodes (89.31 %, 95 %CI = 84.98–92.50), while *Trichostrongylus* was the most prevalent nematode (15.64 %, 95 %CI = 11.74–20.54; Table 1). Most taxa were found to have variance <0.1 (i.e. *Bunostomum*, *Chabertia*, *Haemonchus*, *Moniezia*, *Oesophagostomum*, *Ostertagia*, Paramphistomids, *Strongyloides*, *Trichuris* and *Toxocara*) so were removed from further risk factor analysis.

Median parasite richness was 2 parasite taxa per individual (range 0–9), with dual infection being the most common type of infection (39.31 %, 95 %CI = 33.59–45.34), followed by single infection (21.37 %, 95 %CI = 16.84–26.73; Table 2). Specifically, *Eimeria* combined with Paramphistomids were the most common dual infection, found in 28.24 % of the population (95 %CI = 23.13–33.97; Table S6), followed by *Trichostrongylus* and Paramphistomids (2.67 %, 95 %CI = 1.30–5.41).

Eimeria oocyst counts averaged 144.84 OPG (\pm 215.85; Table S7), with 32.82 % of samples containing less than 50 OPG. Average egg counts were 20.61 EPG (\pm 52.65) for strongyle-type eggs (with 78.24 % of samples containing less than 50 EPG), 11.83 EPG (\pm 36.00) for *Moniezia* (87.02 % of samples containing less than 50 EPG) and 1.91 EPG (\pm 12.99) for *Trichuris* (97.71 % of samples containing less than 50 EPG). Counts of *Trichuris* and *Moniezia* could not be included in further analysis due to their high proportion of zero count data (97.71 % and 87.02 % respectively; Table S7).

Table 1

Number of positive samples and prevalence of each parasite taxa detected in Hong Kong feral cattle fecal samples (n = 262 samples).

	Taxa	Number of positive samples	Prevalence (%)	95 % Confidence interval		
Nematodes	<i>Bunostomum</i>	6	2.29	1.05	–	4.90
	<i>Chabertia</i>	4	1.52	0.59	–	3.85
	<i>Cooperia</i>	30	11.45	8.13	–	15.87
	<i>Dictyocaulus</i>	21	8.01	5.30	–	11.94
	<i>Haemonchus</i>	5	1.91	0.81	–	4.38
	<i>Oesophagostomum</i>	6	2.29	1.05	–	4.90
	<i>Ostertagia</i>	13	4.96	2.92	–	8.30
	<i>Strongyloides</i>	1	0.38	0.01	–	2.12
	<i>Toxocara</i>	1	0.38	0.01	–	2.12
	<i>Trichostrongylus</i>	41	15.64	11.74	–	20.54
	<i>Trichuris</i>	6	2.29	1.05	–	4.90
Trematodes	<i>Fasciola</i>	39	14.88	11.08	–	19.70
	Paramphistomids	234	89.31	84.98	–	92.50
Protozoa	<i>Eimeria</i>	176	67.17	61.27	–	72.57
Cestode	<i>Moniezia</i>	34	12.97	9.43	–	17.58

Confidence Intervals (95%CI) were based on the binomial proportion function 'binconf' in the 'Hmisc' package.

Table 2

Number of samples and prevalence of each count of parasite richness in the Hong Kong feral cattle (n = 262 fecal samples). Parasite richness is expressed as the number of different endoparasite taxa detected per sample.

Parasite richness	Number of samples	Percentage (%)	95 % Confidence interval		
0	5	1.90	0.81	–	4.38
1	56	21.37	16.84	–	26.73
2	103	39.31	33.59	–	45.34
3	63	24.04	19.26	–	29.57
4	23	8.77	5.92	–	12.82
5	6	2.29	1.05	–	4.90
6	3	1.14	0.39	–	3.31
7	1	0.38	0.01	–	2.12
8	1	0.38	0.01	–	2.12
9	1	0.38	0.01	–	2.12

Confidence Intervals (95%CI) were based on the binomial proportion function 'binconf' in the 'Hmisc' package.

3.2. Risk factors for endoparasite infection

3.2.1. Parasite richness

There was an association between provisioning and parasite richness, with provisioned herds having higher parasite richness than groups not provisioned (Risk Ratio RR = 1.53, 95 %CI = 1.20–1.96, $p < 0.0001$). We did not identify associations with any of the other predictor variables.

3.2.2. Parasite prevalence

The prevalence of *Eimeria* was positively associated with wet season conditions, higher parasite richness, provisioning, and larger group size. *Fasciola* prevalence positively correlated with higher parasite richness while demonstrating negative associations with wet season conditions, cattle access to marshlands, and larger group sizes. *Cooperia* prevalence increased with higher parasite richness and was higher in herds with access to marshlands compared to herds that could not access marshlands. *Cooperia* prevalence was also higher in the dry compared to the wet season. *Trichostrongylus* detection rates increased with higher parasite richness but decreased during the wet season and in provisioned herds. Male cattle exhibited a significantly higher prevalence of *Trichostrongylus* infection than females, with males being three times more likely to have *Trichostrongylus* larvae detected in their cultured samples. Comprehensive associations are presented in Table 3.

3.2.3. Parasite counts

Cattle in larger groups were more likely to have *Eimeria* oocysts detected in their feces (OR = 1.05, 95 %CI = 1.01–1.08, $p = 0.03$) and had larger oocyst counts than cattle in smaller groups (RR = 1.02, 95 %

CI = 1.01–1.03, $p < 0.0001$). Strongyle-type eggs were more likely to be detected in feces collected in the wet season than in the dry season (OR = 2.32, 95 % CI = 1.23–4.54, $p = 0.009$). Strongyle-type egg counts were also higher in the wet than in the dry season (RR = 1.40, 95 % CI = 1.02–1.92, $p = 0.001$). No significant sex-based difference was observed in the likelihood of strongyle-type egg detection (OR = 50, 95 % CI = 0.30–10000, $p = 0.13$), but males had higher fecal strongyle-type egg counts than females (RR = 21.29, 95 %CI = 1.96–228.47, $p = 0.01$); this indicates that while both sexes could be infected with strongyle-type eggs, infections in males were more severe in terms of numbers of eggs detected in feces. A significant interaction between sex and body condition effect on fecal strongyle-type egg counts was also found, with strongyle-type egg counts decreasing in males as body condition improved (RR = 0.59, 95 %CI = 0.37–0.94, $p = 0.02$). Detailed associations are presented in Table 4.

4. Discussion

Endoparasite infections can have major implications for individual cattle health in feral/wild populations, and for the maintenance of parasites in natural environments (Budischak et al., 2018; Chrétien et al., 2023; Thapa et al., 2022). HK feral cattle offered a unique opportunity to investigate endoparasite infection in a free-ranging cattle population that does not receive anthelmintic treatments. We evaluated endoparasite infection (richness, prevalence and counts) in 262 samples from 177 cattle from seven herds in the wet and dry seasons. We found a high richness of endoparasites in the HK feral cattle, identifying 15 endoparasite taxa. Infection with one parasite was found to increase infection risk with all parasites, as expressed by association between parasite richness and each parasite taxon prevalence. A higher number of parasite taxa were detected in provisioned herds, alongside a higher likelihood of detection of *Eimeria* oocysts, while *Trichostrongylus* larvae were less prevalent in feces from provisioned herds, reflecting the complexity of provisioning and its consequences in feral/wild populations. Similarly, seasonal variation impacted parasites differently, with *Eimeria* prevalence and strongyle-type egg counts increasing in the wet season, while *Fasciola* eggs, *Cooperia* larvae and *Trichostrongylus* larvae were detected in feces more in the dry season. Group size had complex impacts on endoparasite infection, with larger herds having higher prevalence and counts of *Eimeria* oocysts but lower *Fasciola* egg prevalence. Unlike our expectations, marshland presence decreased *Fasciola* egg prevalence but increased *Cooperia* larval prevalence. Finally, males had higher strongyle-type egg counts than females.

Most cattle were infected simultaneously with multiple parasite taxa, with provisioning being the only risk factor predicting the number of parasite taxa found. The most common dual infection was *Eimeria* combined with Paramphistomids, likely due to the high prevalence of

Table 3

Factors impacting the prevalence of *Eimeria*, *Fasciola*, *Cooperia* and *Trichostrongylus* in Hong Kong feral cattle (n = 262 fecal samples) based on a mixed effects logistic regression. Italics indicate reference category in categorical variables. Bold indicates significant associations.

Response Variable (Pseudo R ²)	Predictor		Odd Ratio	95 %CI			p-value
<i>Eimeria</i> prevalence (0.67)	Richness		4.48	2.75	-	7.28	<0.0001
	Season	Wet	2.54	1.20	-	5.39	0.01
		<i>Dry</i>	<i>Reference</i>				
	Provisioning	Yes	6.13	1.85	-	20.31	0.003
		<i>No</i>	<i>Reference</i>				
	Marshland Access	Yes	3.85	0.66	-	22.45	0.13
		<i>No</i>	<i>Reference</i>				
<i>Fasciola</i> prevalence (0.41)	Group Size		1.07	1.02	-	1.11	0.002
	Richness		1.81	1.35	-	2.42	0.002
	Season	Wet	0.26	0.11	-	0.63	<0.0001
		<i>Dry</i>	<i>Reference</i>				
	Provisioning	Yes	3.80	0.59	-	24.40	0.15
		<i>No</i>	<i>Reference</i>				
	Marshland Access	Yes	0.06	0.01	-	0.36	0.001
	<i>No</i>	<i>Reference</i>					
<i>Cooperia</i> prevalence (0.66)	Group Size		0.94	0.90	-	0.98	0.003
	Richness		4.14	2.56	-	6.70	<0.0001
	Season	Wet	0.01	0.002	-	0.13	<0.0001
		<i>Dry</i>	<i>Reference</i>				
	Marshland Access	Yes	4.05	1.41	-	11.64	0.04
	<i>No</i>	<i>Reference</i>					
<i>Trichostrongylus</i> prevalence (0.69)	Sex	Male	3.13	1.18	-	8.32	0.02
		<i>Female</i>	<i>Reference</i>				
	BCS		0.65	0.29	-	1.46	0.30
	Richness		7.55	3.96	-	14.40	<0.0001
	Season	Wet	0.18	0.06	-	0.54	0.002
		<i>Dry</i>	<i>Reference</i>				
	Provisioning	Yes	0.17	0.03	-	0.94	0.04
		<i>No</i>	<i>Reference</i>				
	Marshland Access	Yes	3.20	0.25	-	40.62	0.36
		<i>No</i>	<i>Reference</i>				
Group Size		1.01	0.95	-	1.08	0.53	

95%CI= Confidence Interval; BCS=Body Condition Score.

Variables presented above reflect final selection resulting from a backward selection process, leading to different variables selected in each model.

Table 4

Factors impacting the fecal counts of *Eimeria* oocysts and of strongyle-types eggs in Hong Kong feral cattle (n = 262 fecal samples) based on the conditional count model and zero-inflation model extracted from mixed effects zero-inflated negative binomial models. Italics indicate reference category in categorical variables. Bold indicates significant associations.

Response Variable (Pseudo R ²)	Predictor		Risk Ratio/Odd Ratio	95 %CI			p-value	Model
<i>Eimeria</i> fecal oocyst counts (0.25)	Sex	Male	0.83	0.67	-	1.03	0.09	Count
		<i>Female</i>	<i>Reference</i>	1.23	0.68	-	2.22	0.49
	Marshland Access	Yes	1.81	0.72	-	1.91	0.49	Count
		<i>No</i>	<i>Reference</i>	0.49	0.13	-	1.78	0.28
	Group Size		1.02	1.01	-	1.03	<0.0001	Count
		1.05	1.01	-	1.08	0.03	ZI	
Strongyle-type fecal egg count (0.22)	Sex	Male	21.19	1.96	-	228.47	0.01	Count
		<i>Female</i>	<i>Reference</i>	50	0.30	-	10000	0.13
	BCS		1.19	0.85	-	1.68	0.30	Count
			1.42	0.34	-	1.42	0.31	ZI
	Interaction Sex – BCS	Male	0.59	0.37	-	0.94	0.02	Count
		<i>Female</i>	<i>Reference</i>	0.54	0.20	-	1.42	0.20
	Season	Wet	1.40	1.02	-	1.92	0.03	Count
		<i>Dry</i>	<i>Reference</i>	2.32	1.23	-	4.54	0.009
	Provisioning	Yes	1.19	0.76	-	1.85	0.43	Count
		<i>No</i>	<i>Reference</i>	1.58	0.58	-	4.16	0.37
	Marshland Access	Yes	1.17	0.51	-	2.66	0.70	Count
		<i>No</i>	<i>Reference</i>	1.88	0.37	-	10	0.45
	Group Size		1.00	0.98	-	1.02	0.94	Count
		<i>Reference</i>	1.00	0.96	-	1.04	0.78	ZI

95%CI= Confidence Interval; BCS=Body Condition Score; Odd Ratios are reversed to indicate the probability of non-zero values; Count = conditional model for non-zero counts; ZI = zero-inflation.

both parasites in the population. In HK feral cattle, the positive relationship between parasite richness and provisioning suggests that provisioning does not protect individuals from infection. This finding is consistent with observations in provisioned wild boars (*Sus scrofa*: Navarro-Gonzalez et al., 2013). Provisioning can amplify pathogen invasion by increasing host aggregation and contact rates (Becker et al., 2015; Murray et al., 2016), which in turn results in higher individual exposure to infective material (Becker et al., 2015) as observed in red deer (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*; Miller et al., 2003; Vicente et al., 2007). Co-infections are widespread in wild ruminant populations and interact with individual fitness through two primary mechanisms, intra-host resource competition and immune-mediated interactions (Bashey, 2015; Ezenwa, 2021; Morris et al., 2019). While the prevalence of most taxa was associated with parasite richness, further investigation is required to understand the mechanisms involved; notably to discriminate simple association (Poulin, 1996) from dynamic intra-host parasite interactions (Bashey, 2015; Ezenwa, 2021; Morris et al., 2019).

Interestingly, we found that HK feral cattle carry a high richness and prevalence of endoparasites, while egg and oocysts counts are low. In organic cattle farms with little to no anthelmintic treatments and mixed-age grazing practices, high prevalence of endoparasites and low egg counts were also found (Hördegen, 2005). Some ruminants are known to create resistance to infection by carrying a low load of each endoparasite taxon to enhance their immune response, as observed for some taxa of protozoa (Hansen and Perry, 1994; Taylor, 2000), cestodes (Almeida-Cacedo et al., 2023) and nematodes (Parker et al., 2020; Parkinson et al., 2019). Measuring immune response (Alvarez Rojas et al., 2015; Höglund, 2010; Moreau and Chauvin, 2010; Motran et al., 2018) could help quantify the magnitude of immunity and the impact of low counts on the immune responses of the HK feral cattle.

We found low *Eimeria* oocyst counts, the only protozoa taxon detected in our population. Adult cattle are expected to develop immunity to *Eimeria* by sustaining consistently low levels of infection (leading to low FOC) throughout their lives, resulting in a high prevalence of the infection with minimal clinical symptoms (Hansen and Perry, 1994; Taylor, 2000). No individuals had oocyst counts of >5000 OPG, indicating that clinical signs are unlikely (Radostits et al., 2007), further supported by the absence of impact on body condition in our study. This is similar to findings in organic cattle farms in Switzerland, where prevalence of *Eimeria* averaged 45.5 % but did not lead to clinical signs (Hördegen, 2005). While protozoan counts were not affected by season, the prevalence of *Eimeria* was higher in the wet season than in the dry season. In HK feral cattle, provisioned large herds were more infected with protozoa, possibly due to increased host density and reduced roaming behavior (Becker et al., 2015; Murray et al., 2016) leading to increased pasture contamination and higher individual exposure to infective *Eimeria* oocysts in these provisioned cattle.

Fasciola infections were more prevalent in the dry season. Snails may concentrate around natural water sources which provide grazing opportunities for ruminants during drier months (Hansen and Perry, 1994), thereby increasing host exposure to *Fasciola* infection during these months (Radostits et al., 2007). Additionally, *Fasciola* adults only produce eggs two to four months after being ingested (Cornelissen et al., 2001; Parkinson et al., 2019; Pilarczyk et al., 2021), suggesting that HK feral cattle may become infected in the wet season, leading to higher detection of *Fasciola* eggs in their feces during the dry season. Although lymnaeid snails have been identified in HK, their seasonal distribution has not been investigated (Habib et al., 2018; Hau et al., 2018). Unexpectedly, we also found that *Fasciola* infections were more common in cattle not grazing in marshlands. This may be due to increased presence of predators of intermediate hosts (such as egrets and crabs feeding on invertebrates in HK marshlands; Dudgeon and Corlett, 2010; Pang et al., 2020; Wong et al., 2001) and intra-host competition in snails between trematodes sharing an intermediate host (Lagrué et al., 2007; Lagrué and Poulin, 2008; Leung and Poulin, 2011) in marshlands. Similarly, the

negative relationship between *Fasciola* prevalence and group size may reflect the dependence of infection rate on snail density rather than cattle density. If we assume a constant trematode density across the environment, then individuals in larger herds have lower probabilities of ingesting infective material than individuals in smaller herds (Khalil et al., 2016). Additionally, increased diversity of intermediate host species has been found to decrease parasite transmission by 78 % (Johnson et al., 2013). Investigation of snail-focused factors (e.g., diversity and seasonality of trematode infections in snail populations) could improve our understanding of trematode infection in feral cattle.

Strongyle-type eggs were the most prevalent nematode eggs in HK feral cattle. Our study extracted risk factors for *Trichostrongylus* prevalence, *Cooperia* prevalence and strongyle-type egg counts. Most strongyle-type egg counts were low (below 200 EPG), with only seven out of 262 samples showing moderate infections (200–800 EPG) and no heavy infections detected (Hansen and Perry, 1994; Parkinson et al., 2019). Strongyle-type egg counts were higher in the wet season, consistent with previous findings in farmed cattle (Forbes, 2018) and wild ruminants (Corlatti et al., 2012; Turner et al., 2012); while the prevalence of *Trichostrongylus* and *Cooperia* larvae was higher in the dry season. This discrepancy may result from limitations in our methodology, which did not allow for taxon-specific count estimations. Additionally, strongyle-type egg counts and *Trichostrongylus* larval prevalence were higher in males than females, similar to findings in other wild ruminants such as red deer (Albery et al., 2018). Strongyle-type egg counts were negatively related to body condition in males, similar to findings in feral horses (Debeffe et al., 2016) and Cambodian farmed cattle (Dorny et al., 2011), but we could not determine the causality of the relationship between body condition and strongyle-type egg counts.

While our methodology provides valuable information on the epidemiology of endoparasites in a feral cattle population using non-invasive sampling techniques, wider adoption of such methods may be challenging. Indeed, in order to collect fecal samples in free-ranging individuals without handling, extensive observations of these animals were required, making it very time consuming. Additionally, long-term information on individual phenotypes (e.g., a photo-catalogue) was required for identification of individuals throughout different seasons. Knowledge of cattle habitat and movement behavior was also necessary to find such free-ranging cattle. Using freshly voided feces also necessitates discarding parts of the sample that touch the ground to avoid potential contamination from the soil, and at times being unable to obtain a sample when individuals were standing nearby making collection unsafe. However, in the context of feral and wild populations, limiting capture and handling is essential to ensure long-term population viability, with several physiological impacts and welfare implications associated with capture (Cattet et al., 2008; Kongsurakan et al., 2020). Therefore, although challenging, such non-invasive methodologies do offer advantages.

5. Conclusion

Our research highlights the epidemiology of endoparasite infection in a subtropical feral cattle population not receiving anthelmintic treatments. We identified taxon-specific risk factors and seasonal patterns of infection. Most cattle fecal samples contained multiple parasite taxa simultaneously. Sex and body condition had limited impact on endoparasite infection and mostly impacted nematode infections. Provisioning and herd size were important risk factors, showing contrasting impacts on endoparasite infections at genus level. Provisioning is used in wild and feral population management and human-animal conflict mitigation, although its consequences can be hard to assess. Thus, our results can inform the impact of such actions in ruminants under limited management. Our findings deepen the understanding of individual variations in infection risk in free-ranging ruminants and parasite ecology in subtropical climates.

CRedit authorship contribution statement

Tania A. Perroux: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Samantha S.Y. Lie:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Alan G. McElligott:** Writing – review & editing, Methodology. **Danchen A. Yang:** Writing – review & editing, Formal analysis. **Fraser I. Hill:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **George M.W. Hodgson:** Writing – review & editing, Methodology. **Wing S. Wong:** Writing – review & editing, Methodology. **Kate J. Flay:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the Writing process

The first author being a non-native English speaker, contents were first drafted then AI was used to improve readability and language of some sections with CityU GPT chatbot powered by Microsoft Azure OpenAI. After using this tool/service, all authors reviewed and edited the content and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

- Ades, G., Nip, T., Woo, M.C., 2013. Ecological and Conservation Importance of Six Sai Kung Country Park Enclaves. Kadoorie Farm and Botanical Gardens. AFCD, 2018. Stray cattle and Buffalo management plan [WWW Document] Agric. Fish. Conserv. Dep. <https://www.afcd.gov.hk/english/quarantine/cattlebuffalo.html>. (Accessed 6 May 2023).
- Akinyi, M.Y., Jansen, D., Habig, B., Gesquiere, L.R., Alberts, S.C., Archie, E.A., 2019. Costs and drivers of helminth parasite infection in wild female baboons. *J. Anim. Ecol.* 88, 1029–1043. <https://doi.org/10.1111/1365-2656.12994>.
- Albery, G.F., Kenyon, F., Morris, A., Morris, S., Nussey, D.H., Pemberton, J.M., 2018. Seasonality of helminth infection in wild red deer varies between individuals and between parasite taxa. *Parasitology* 145, 1410–1420. <https://doi.org/10.1017/S0031182018000185>.
- Allwin, B., 2015. Prevalence of gastrointestinal parasites in Gaur (*Bos gaurus*) and domestic cattle at interface zones of the Nilgiri Hills, Tamil Nadu, India. *J. Vet. Sci. Technol.* 07. <https://doi.org/10.4172/2157-7579.1000280>.
- Almeida-Caicedo, M.G., Almeida Secaira, R.I., Nuñez Torres, O.P., Borja-Caicedo, B.E., 2023. *Moniezia expansa* y *Moniezia benedeni* una parasitosis en ruminantes: una visión general de sus aspectos vinculados a su taxonomía. *J. Selva Andina Anim. Sci.* 10, 130–138. <https://doi.org/10.36610/j.jsaas.2023.100200130>.
- Alvarez Rojas, C.A., Ansell, B.R., Hall, R.S., Gasser, R.B., Young, N.D., Jex, A.R., Scheerlinck, J.P.-Y., 2015. Transcriptional analysis identifies key genes involved in metabolism, fibrosis/tissue repair and the immune response against *Fasciola hepatica* in sheep liver. *Parasites Vectors* 8, 124. <https://doi.org/10.1186/s13071-015-0715-7>.
- Aragaw, K., Tilahun, H., 2019. Coprological study of trematode infections and associated host risk factors in cattle during the dry season in and around Bahir Dar, northwest Ethiopia. *Vet. Anim. Sci.* 7, 100041. <https://doi.org/10.1016/j.vas.2018.11.002>.

- Barbato, M., Reichel, M.P., Passamonti, M., Low, W.Y., Colli, L., Tearle, R., Williams, J.L., Ajmone Marsan, P., 2020. A genetically unique Chinese cattle population shows evidence of common ancestry with wild species when analysed with a reduced ascertainment bias SNP panel. *PLoS One* 15, e0231162. <https://doi.org/10.1371/journal.pone.0231162>.
- Bashley, F., 2015. Within-host competitive interactions as a mechanism for the maintenance of parasite diversity. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20140301. <https://doi.org/10.1098/rstb.2014.0301>.
- Becker, D.J., Streicker, D.G., Altizer, S., 2015. Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. *Ecol. Lett.* 18, 483–495. <https://doi.org/10.1111/ele.12428>.
- Berteaux, D., Micol, T., 1992. Population studies and reproduction of the feral cattle (*Bos taurus*) of Amsterdam Island, Indian Ocean. *J. Zool.* 228, 265–276. <https://doi.org/10.1111/j.1469-7998.1992.tb04607.x>.
- Bostal, F., Scorolli, A.L., Zalba, S.M., 2024. Seasonal variation of body condition in feral horses at Tornquist Park, Southern Pampas, Argentina. *Eur. J. Wildl. Res.* 70, 16. <https://doi.org/10.1007/s10344-024-01767-6>.
- Brooks, M.E., Kristensen, K., Benthem, K.J., van Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9, 378. <https://doi.org/10.32614/RJ-2017-066>.
- Budischak, S.A., O’Neal, D., Jolles, A.E., Ezenwa, V.O., 2018. Differential host responses to parasitism shape divergent fitness costs of infection. *Funct. Ecol.* 32, 324–333. <https://doi.org/10.1111/1365-2435.12951>.
- Cattadori, I.M., Boag, B., Hudson, P.J., 2008. Parasite co-infection and interaction as drivers of host heterogeneity. *Int. J. Parasitol.* 38, 371–380. <https://doi.org/10.1016/j.ijpara.2007.08.004>.
- Cattet, M., Boulanger, J., Stenhouse, G., Powell, R.A., Reynolds-Hogland, M.J., 2008. An evaluation of long-term capture effects in Ursids: implications for wildlife welfare and research. *J. Mammal.* 89 (1), 973–990. <https://doi.org/10.1644/08-MAMM-A-095>.
- Cezaro, M.C., Neves, J.H., Cury, J.R.L.M., Dalanezi, F.M., Oliveira, R.M., Ferreira, J.C.P., Neto, V.A.K., Schmidt, E.M.S., 2018. Gastrointestinal and pulmonary nematodes in calves naturally infected in the cities of Botucatu and Manduri, in the Brazilian state of São Paulo. *Pesqui. Veterinária Bras* 38, 1286–1292. <https://doi.org/10.1590/1678-5150-pvb-5225>.
- Chrétien, E., De Bonville, J., Guitard, J., Binning, S.A., Melis, É., Kack, A., Côté, A., Gradito, M., Papillon, A., Thelamon, V., Levet, M., Barou-Dagues, M., 2023. Few studies of wild animal performance account for parasite infections: a systematic review. *J. Anim. Ecol.* 92, 794–806. <https://doi.org/10.1111/1365-2656.13864>.
- Cizauskas, C.A., Turner, W.C., Pitts, N., Getz, W.M., 2015. Seasonal patterns of hormones, Macroparasites, and Microparasites in wild African ungulates: the interplay among stress, reproduction, and disease. *PLoS One* 10, e0120800. <https://doi.org/10.1371/journal.pone.0120800>.
- Cockrill, W.R., 1976. The Buffaloes of China. Food Agric. Organization United Nations, Italy. <https://catalogue.nla.gov.au/catalog/590030>.
- Colston, M., Mearns, R., 2023. Liver fluke in cattle and sheep: getting ahead of a rapidly adapting parasite. In: *Pract.* 45, pp. 332–343. <https://doi.org/10.1002/inpr.341>.
- Corlatti, L., Béthaz, S., Von Hardenberg, A., Bassano, B., Palme, R., Lovari, S., 2012. Hormones, parasites and male mating tactics in Alpine chamois: identifying the mechanisms of life history trade-offs. *Anim. Behav.* 84, 1061–1070. <https://doi.org/10.1016/j.anbehav.2012.08.005>.
- Cornelissen, J.B.W.J., Gaasenbeek, C.P.H., Borgsteede, F.H.M., Holland, W.G., Harmsen, M.M., Boersma, W.J.A., 2001. Early immunodiagnosis of fasciolosis in ruminants using recombinant *Fasciola hepatica* cathepsin L-like protease. *Int. J. Parasitol.* 31, 728–737. [https://doi.org/10.1016/S0020-7519\(01\)00175-8](https://doi.org/10.1016/S0020-7519(01)00175-8).
- Debeffe, L., McCloughlin, P.D., Medill, S.A., Stewart, K., Andres, D., Shury, T., Wagner, B., Jenkins, E., Gilleard, J.S., Poissant, J., 2016. Negative covariance between parasite load and body condition in a population of feral horses. *Parasitology* 143, 983–997. <https://doi.org/10.1017/S0031182016000408>.
- D’Ochchio, M.J., Baruselli, P.S., Campanile, G., 2019. Influence of nutrition, body condition, and metabolic status on reproduction in female beef cattle: a review. *Theriogenology* 125, 277–284. <https://doi.org/10.1016/j.theriogenology.2018.11.010>.
- Dorny, P., Stolaroff, V., Charlier, J., Meas, S., Sorn, S., Chea, B., Holl, D., Van Aken, D., Vercurryse, J., 2011. Infections with gastrointestinal nematodes, *Fasciola* and *Paramphistomum* in cattle in Cambodia and their association with morbidity parameters. *Vet. Parasitol.* 175, 293–299. <https://doi.org/10.1016/j.vetpar.2010.10.023>.
- Dudgeon, D., Chan, E., 1996. Ecological Study of Freshwater Wetland Habitats in Hong Kong.
- Dudgeon, D., Corlett, R., 2010. Hills and Streams: an Ecology of Hong Kong. Hong Kong University Press, Hong Kong.
- El-Tahawy, A.S., Bazh, E.K., Khalafalla, R.E., 2017. Epidemiology of bovine fascioliasis in the Nile Delta region of Egypt: its prevalence, evaluation of risk factors, and its economic significance. *Vet. World* 10, 1241–1249. <https://doi.org/10.14202/vetworld.2017.1241-1249>.
- Ezenwa, V.O., 2021. Co-Infection and nutrition: integrating ecological and epidemiological perspectives. In: Humphries, D.L., Scott, M.E., Vermund, S.H. (Eds.), *Nutrition and Infectious Diseases*. Springer International Publishing, Cham, pp. 411–428. https://doi.org/10.1007/978-3-030-56913-6_14.
- Ezenwa, V.O., 2003. Habitat overlap and gastrointestinal parasitism in sympatric African bovines. *Parasitology* 126, 379–388. <https://doi.org/10.1017/S0031182002002913>.
- Ezenwa, V.O., Worsley-Tonks, K.E.L., 2018. Social living simultaneously increases infection risk and decreases the cost of infection. *Proc. R. Soc. B Biol. Sci.* 285, 20182142. <https://doi.org/10.1098/rspb.2018.2142>.

- Food and Agriculture Organization of the United Nations, 2021. FAOSTAT. <https://www.fao.org/faostat/en/#data/QCL> [WWW Document]. Food Agric. Organ. U. N. URL(accessed 9.21.23).
- Forbes, A., 2018. Lungworm in cattle: epidemiology, pathology and immunobiology. *Livestock* 23, 59–66. <https://doi.org/10.12968/live.2018.23.2.59>.
- Fox, G.A., Negrete-Yankelevich, S., Sosa, V.J., 2015. *Ecological Statistics: Contemporary Theory and Application*. Oxford university press, Oxford.
- Geurden, T., Somers, R., Thanh, N.T.G., Vien, L.V., Nga, V.T., Giang, H.H., Dorny, P., Giao, H.K., Vercruyse, J., 2008. Parasitic infections in dairy cattle around Hanoi, northern Vietnam. *Vet. Parasitol.* 153, 384–388. <https://doi.org/10.1016/j.vetpar.2008.01.031>.
- Gibbons, L.M., Jacobs, D.E., Fox, M.T., 2022. The RVC/FAO guide on veterinary diagnostic Parasitology [WWW Document]. URL <https://www.rvc.ac.uk/review/parasitology/index/index.htm>, 10.25.23.
- Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y.M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E., Milo, R., 2023. The global biomass of wild mammals. *Proc. Natl. Acad. Sci. USA* 120, e2204892120. <https://doi.org/10.1073/pnas.2204892120>.
- Griffin, R.H., Nunn, C.L., 2012. Community structure and the spread of infectious disease in primate social networks. *Evol. Ecol.* 26, 779–800. <https://doi.org/10.1007/s10682-011-9526-2>.
- Habib, M.R., Lv, S., Guo, Y.-H., Gu, W.-B., Standley, C.J., Caldeira, R.L., Zhou, X.-N., 2018. Morphological and molecular characterization of invasive *Biomphalaria straminea* in southern China. *Infect. Dis. Poverty* 7, 120. <https://doi.org/10.1186/s40249-018-0505-5>.
- Hall, S.J.G., Brenig, B., Ashdown, R.A., Curry, M.R., 2021. Conservation of rare wild-living cattle *Bos taurus* (L.): coat colour gene illuminates breed history, and associated reproductive anomalies have not reduced herd fertility. *J. Zool. jzo* 12929. <https://doi.org/10.1111/jzo.12929>.
- Hansen, J., Perry, B.D., 1994. *The Epidemiology, Diagnosis and Control of Helminth Parasites of Ruminants. A Handbook*. International Laboratory for Research on Animal Diseases, Kenya.
- Hau, B.C.H., Lo, K.W.F., So, K.Y.K., 2018. *Living Water and Community Revitalization-An Agricultural-Led Action, Engagement and Incubation Programme at Lai Chi Wo: Biodiversity Baseline and Management Plan of Freshwater and Terrestrial Habitats of Lai Chi Wo*. Hong Kong: Policy for Sustainability Lab. Faculty of Social Sciences, The University of Hong Kong, Hong Kong.
- Heinze, G., Wallisch, C., Dunkler, D., 2018. Variable selection – a review and recommendations for the practicing statistician. *Biom. J.* 60, 431–449. <https://doi.org/10.1002/bimj.201700067>.
- Hewison, A.J.M., Bonnot, N.C., Gaillard, J.-M., Kjellander, P., Lemaitre, J.-F., Morellet, N., Pellerin, M., 2024. Body mass change over winter is consistently sex-specific across roe deer (*Capreolus capreolus*) populations. *Peer Community J.* 4, e98. <https://doi.org/10.24072/pcjournal.479>.
- Hines, A.M., Ezenwa, V.O., Cross, P., Rogerson, J.D., 2007. Effects of supplemental feeding on gastrointestinal parasite infection in elk (*Cervus elaphus*): preliminary observations. *Vet. Parasitol.* 148, 350–355. <https://doi.org/10.1016/j.vetpar.2007.07.006>.
- Hodgson, G.M.W., Flay, K.J., Perroux, T.A., Chan, W.Y., McElligott, A.G., 2024. Sex and dominance status affect allogrooming in free-ranging feral cattle. *Anim. Behav.* 210, 275–287. <https://doi.org/10.1016/j.anbehav.2023.12.020>.
- Höglund, J., 2010. Parasite surveillance and novel use of anthelmintics in cattle. *Acta Vet. Scand.* 52, S25. <https://doi.org/10.1186/1751-0147-52-S1-S25>.
- Hördegen, P., 2005. *Epidemiology of Internal Parasites on Swiss Organic Dairy Farms and Phytotherapy as a Possible Worm Control Strategy (Doctoral Dissertation)*. ETH Zurich, Switzerland.
- Hsieh, F.Y., Bloch, D.A., Larsen, M.D., 1998. A simple method of sample size calculation for linear and logistic regression. *Stat. Med.* 17, 1623–1634.
- Huang, C.-C., Wang, L.-C., Pan, C.-H., Yang, C.-H., Lai, C.-H., 2014. Investigation of gastrointestinal parasites of dairy cattle around Taiwan. *J. Microbiol. Immunol. Infect.* 47, 70–74. <https://doi.org/10.1016/j.jmii.2012.10.004>.
- Johnson, P.T.J., Preston, D.L., Hoverman, J.T., Richgels, K.L.D., 2013. Biodiversity decreases disease through predictable changes in host community competence. *Nature* 494, 230–233. <https://doi.org/10.1038/nature11883>.
- Jones, G.G., Sadler, P., 2012. A review of published sources for age at death in cattle. *Environ. Archaeol.* 17, 1–10. <https://doi.org/10.1179/1461410312Z.00000000011>.
- Kaewthamasorn, M., Wongsamee, S., 2006. A preliminary survey of gastrointestinal and haemoparasites of beef cattle in the tropical livestock farming system in Nan Province, northern Thailand. *Parasitol. Res.* 99, 306–308. <https://doi.org/10.1007/s00436-006-0148-5>.
- Khalil, H., Ecker, F., Evander, M., Magnusson, M., Hörnfeldt, B., 2016. Declining ecosystem health and the dilution effect. *Sci. Rep.* 6, 31314. <https://doi.org/10.1038/srep31314>.
- Kotoldziej-Sobocińska, M., 2019. Factors affecting the spread of parasites in populations of wild European terrestrial mammals. *Mammal Res* 64, 301–318. <https://doi.org/10.1007/s13364-019-00423-8>.
- Koltz, A.M., Civitello, D.J., Becker, D.J., Deem, S.L., Classen, A.T., Barton, B., Brenn-White, M., Johnson, Z.E., Kutz, S., Malishev, M., Preston, D.L., Vannatta, J.T., Penczykowski, R.M., Ezenwa, V.O., 2022. Sublethal effects of parasitism on ruminants can have cascading consequences for ecosystems. *Proc. Natl. Acad. Sci.* 119, e2117381119. <https://doi.org/10.1073/pnas.2117381119>.
- Kongsurakan, P., Chaiyarat, R., Nakbun, S., Thongthip, N., Anuracpreeda, P., 2020. Monitoring body condition score of reintroduced banteng (*Bos javanicus* D'Alton, 1923) into Salakphra Wildlife Sanctuary, Thailand. *PeerJ* 8, e9041. <https://doi.org/10.7717/peerj.9041>.
- Laguer, C., McEwan, J., Poulin, R., Keeney, D.B., 2007. Co-occurrences of parasite clones and altered host phenotype in a snail-trematode system. *Int. J. Parasitol.* 37, 1459–1467. <https://doi.org/10.1016/j.ijpara.2007.04.022>.
- Laguer, C., Poulin, R., 2008. Intra- and interspecific competition among helminth parasites: effects on *Coitocaeum parvum* life history strategy, size and fecundity. *Int. J. Parasitol.* 38, 1435–1444. <https://doi.org/10.1016/j.ijpara.2008.04.006>.
- Legislative Council Panel on Food Safety and Environmental Hygiene, 2017. *Feral Cattle Care and Welfare Issues in Sai Kung*.
- Leung, T.L.F., Poulin, R., 2011. Intra-host competition between co-infecting digenaeans within a bivalve second intermediate host: dominance by priority-effect or taking advantage of others? *Int. J. Parasitol.* 41, 449–454. <https://doi.org/10.1016/j.ijpara.2010.11.004>.
- Loginova, O.A., Rozenfeld, S.B., Sipko, T.P., Mizin, I.A., Panchenko, D.V., Laishev, K.A., Bondar, M.G., Kolpashchikov, L.A., Gruzdev, A.R., Kulemeev, P.S., Litovka, D.I., Semerikova, M.N., Mamontov, V.N., Mamaev, E.G., Spiridonov, S.E., 2023. Diversity and distribution of helminths in wild ruminants of the Russian Arctic: Reindeer (*Rangifer tarandus*), Muskoxen (*Ovibos moschatus*), and snow sheep (*Ovis nivicola*). *Diversity* 15, 672. <https://doi.org/10.3390/d15050672>.
- MacPhee, R.D., Greenwood, A.D., 2013. Infectious disease, endangerment, and extinction. *Int. J. Evol. Biol.* 2013.
- Masho, W., Banerjee, S., Taye, M., Admasu, Z., Baye, M., 2022. Assessment of indigenous Shaka cattle structural indices reared in Shaka zone, south west Ethiopia. *Heliyon* 8, e09212. <https://doi.org/10.1016/j.heliyon.2022.e09212>.
- McElligott, A.G., Naulty, F., Clarke, W.V., Hayden, T.J., 2003. The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* <https://doi.org/10.5167/UZH-402>.
- Miller, R., Kaneene, J.B., Fitzgerald, S.D., Schmitt, S.M., 2003. Evaluation of the influence of supplemental feeding of white-tailed deer (*Odocoileus virginianus*) on the prevalence of bovine tuberculosis in the Michigan wild deer population. *J. Wildl. Dis.* 39, 84–95. <https://doi.org/10.7589/0090-3558-39.1.84>.
- Milner, J.M., Van Beest, F.M., Schmidt, K.T., Brook, R.K., Storaa, T., 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates: effects of Feeding Ungulates. *J. Wildl. Manag.* 78, 1322–1334. <https://doi.org/10.1002/jwmg.798>.
- Moreau, E., Chauvin, A., 2010. Immunity against helminths: interactions with the host and the intercurrent infections. *J. Biomed. Biotechnol.* 2010, 1–9. <https://doi.org/10.1155/2010/428593>.
- Morris, T.C., Van Der Ploeg, J., Bih Awa, S., Van Der Lingen, C.D., Reed, C.C., 2019. Parasite community structure as a predictor of host population structure: an example using *Callorhynchus capensis*. *Int. J. Parasitol. Parasites Wildl.* 8, 248–255. <https://doi.org/10.1016/j.ijppaw.2019.03.007>.
- Motran, C.C., Silvane, L., Chiapello, L.S., Theumer, M.G., Ambrosio, L.F., Volpini, X., Celas, D.P., Cervi, L., 2018. Helminth infections: recognition and modulation of the immune response by innate immune cells. *Front. Immunol.* 9, 664. <https://doi.org/10.3389/fimmu.2018.00664>.
- Müller-Klein, N., Heistermann, M., Strube, C., Franz, M., Schülke, O., Ostner, J., 2019. Exposure and susceptibility drive reinfection with gastrointestinal parasites in a social primate. *Funct. Ecol.* 33, 1088–1098. <https://doi.org/10.1111/1365-2435.13313>.
- Murray, M.H., Becker, D.J., Hall, R.J., Hernandez, S.M., 2016. Wildlife health and supplemental feeding: a review and management recommendations. *Biol. Conserv.* 204, 163–174. <https://doi.org/10.1016/j.biocon.2016.10.034>.
- Mushonga, B., Shinexuugi, I., Mbiri, P., Samkange, A., Madzingira, O., Kandiwa, E., 2020. Applicability of teeth examination as a tool for age estimation in a semi-arid cattle production environment in Namibia. *Trop. Anim. Health Prod.* 52, 1649–1654. <https://doi.org/10.1007/s11250-019-02172-x>.
- Navarro-Gonzalez, N., Fernández-Llario, P., Pérez-Martín, J.E., Mentaberre, G., López-Martín, J.M., Lavín, S., Serrano, E., 2013. Supplemental feeding drives endoparasite infection in wild boar in Western Spain. *Vet. Parasitol.* 196, 114–123. <https://doi.org/10.1016/j.vetpar.2013.02.019>.
- Pang, C., Sung, Y.-H., Chung, Y., Ying, H., Fong, H.H.N., Yu, Y., 2020. Spatial ecology of little egret (*Egretta garzetta*) in Hong Kong uncovers preference for commercial fishponds. *PeerJ* 8, e9893. <https://doi.org/10.7717/peerj.9893>.
- Parker, J.M., Goldenberg, S.Z., Letitiya, D., Wittemyer, G., 2020. Stronglyid infection varies with age, sex, movement and social factors in wild African elephants. *Parasitology* 147, 348–359. <https://doi.org/10.1017/S0031182019001653>.
- Parkinson, T.J., Vermunt, J.J., Malmo, J., Laven, R., 2019. *Diseases of Cattle in Australasia*, second ed. Massey University Press, New Zealand.
- Pasquini, C., Pasquini, S., 2004. *Guide to bovine clinics*. In: Pilot Point, TX, fourth ed. Sudz Publishing.
- Patra, G., Efimova, M.A., Sahara, A., Borthakur, S.K., Ghosh, S., Behera, P., Polley, S., Debbarma, A., 2022. Incidence of ecto- and endo-parasitic fauna in small wild ruminants from North Eastern region of India. *Biol. Rhythm Res.* 53, 185–196. <https://doi.org/10.1080/09291016.2019.1628401>.
- Pei, K.J.-C., Lai, Y.-C., Corlett, R.T., Suen, K.-Y., 2010. The larger mammal fauna of Hong Kong: species survival in a highly degraded landscape. *Zool. Stud.* 49, 253–264.
- Perroux, T.A., Lie, S.S.Y., McElligott, A.G., Hill, F.I., Hodgson, G.M.W., Wong, W.W.S., Flay, K.J., 2023. Epidemiology and risk factors for endoparasite infection in subtropical feral cattle in Hong Kong. <https://doi.org/10.17605/OSF.IO/EQ6CY>.
- Perroux, T.A., McElligott, A.G., Hodgson, G.M.W., Flay, K.J., 2025. Seasonal changes in coat colour and sexual size dimorphism in a subtropical ungulate. *bioRxiv*. Preprint. <https://doi.org/10.1101/2025.02.10.637565>.
- Pilarczyk, B., Tomza-Marciniak, A., Pilarczyk, R., Bombik, E., Seremak, B., Udała, J., Sadowska, N., 2021. A comparison of the prevalence of the parasites of the digestive tract in goats from organic and conventional farms. *Animals* 11, 2581. <https://doi.org/10.3390/ani11092581>.

- Pinkham, R., Koon, K.-K., To, J., Chan, J., Vial, F., Gomm, M., Eckery, D.C., Massei, G., 2022. Long-term effect of a GnRH-based immunocontraceptive on feral cattle in Hong Kong. *PLoS One* 17, e0272604. <https://doi.org/10.1371/journal.pone.0272604>.
- Poulin, R., 1996. Richness, nestedness, and randomness in parasite infracommunity structure. *Oecologia* 105, 545–551. <https://doi.org/10.1007/BF00330018>.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing.
- Radostits, O.M., Gay, C.C., Hinchcliff, K.W., Constable, P.D. (Eds.), 2007. *Veterinary Medicine: a Textbook of the Diseases of Cattle, Sheep, Pigs, Goats, and Horses*, tenth ed. Elsevier Saunders, New York.
- Rahman, H., Pal, P., Bandyopadhyay, S., Chatlod, L.R., 2012. Epidemiology of gastrointestinal parasitism in cattle in Sikkim. *Indian J. Anim. Sci.* 151, 88.
- Sánchez, C.A., Becker, D.J., Teitelbaum, C.S., Barriga, P., Brown, L.M., Majewska, A.A., Hall, R.J., Altizer, S., 2018. On the relationship between body condition and parasite infection in wildlife: a review and meta-analysis. *Ecol. Lett.* 21, 1869–1884. <https://doi.org/10.1111/ele.13160>.
- Shaw, A.K., Sherman, J., Barker, F.K., Zuk, M., 2018. Metrics matter: the effect of parasite richness, intensity and prevalence on the evolution of host migration. *Proc. R. Soc. B Biol. Sci.* 285, 20182147. <https://doi.org/10.1098/rspb.2018.2147>.
- Singh, N.K., Singh, H., Jyoti, Haque, M., Rath, S.S., 2012. Prevalence of parasitic infections in cattle of Ludhiana district, Punjab. *J. Parasit. Dis.* 36, 256–259. <https://doi.org/10.1007/s12639-012-0119-y>.
- So, K.Y.K., Dudgeon, D., 2020. Conservation management of abandoned paddy fields in Asia: semi-natural marshes with low-intensity bovid grazing have higher biodiversity. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 30, 1934–1944. <https://doi.org/10.1002/aqc.3442>.
- Sun, P., Wronski, T., Bariyanga, J.D., Apio, A., 2018. Gastro-intestinal parasite infections of Ankole cattle in an unhealthy landscape: an assessment of ecological predictors. *Vet. Parasitol.* 252, 107–116. <https://doi.org/10.1016/j.vetpar.2018.01.023>.
- Sweeny, A.R., Albery, G.F., 2022. Exposure and susceptibility: the twin pillars of infection. *Funct. Ecol.* 36, 1713–1726. <https://doi.org/10.1111/1365-2435.14065>.
- Taylor, M., 2000. Protozoal disease in cattle and sheep. In: *Pract.* 22, pp. 604–617. <https://doi.org/10.1136/inpract.22.10.604>.
- Thapa, B., Parajuli, R.P., Dhakal, P., 2022. Prevalence and burden of gastrointestinal parasites in stray cattle of the Kathmandu Valley. *J. Parasit. Dis.* 46, 845–853. <https://doi.org/10.1007/s12639-022-01499-x>.
- Thompson, R.A., 2013. Parasite zoonoses and wildlife: one health, spillover and human activity. *Int. J. Parasitol.* 43, 1079–1088.
- Thompson, R.C.A., Lymbery, A.J., Smith, A., 2010. Parasites, emerging disease and wildlife conservation. *Int. J. Parasitol.* 40, 1163–1170.
- Thumbi, S.M., Bronsvort, B.M.D.C., Poole, E.J., Kiara, H., Toye, P.G., Mbole-Kariuki, M. N., Conradie, I., Jennings, A., Handel, I.G., Coetzer, J.A.W., Steyl, J.C.A., Hanotte, O., Woolhouse, M.E.J., 2014. Parasite Co-infections and their impact on survival of indigenous cattle. *PLoS One* 9, e76324. <https://doi.org/10.1371/journal.pone.0076324>.
- Titcomb, G.C., Amooni, G., Mantas, J.N., Young, H.S., 2021. The effects of herbivore aggregations at water sources on savanna plants differ across soil and climate gradients. *Ecol. Appl.* 31. <https://doi.org/10.1002/eap.2422>.
- Tung, K.-C., Huang, C.-C., Pan, C.-H., Yang, C.-H., Lai, C.-H., 2012. Prevalence of gastrointestinal parasites in yellow cattle between Taiwan and its Offshore Islands. *Thai J. Vet. Med.* 42, 219–224. <https://doi.org/10.56808/2985-1130.2386>.
- Turner, W.C., Getz, W.M., 2010. Seasonal and demographic factors influencing gastrointestinal parasitism in ungulates of Etosha National Park. *J. Wildl. Dis.* 46, 1108–1119.
- Turner, W.C., Versfeld, W.D., Kilian, J.W., Getz, W.M., 2012. Synergistic effects of seasonal rainfall, parasites and demography on fluctuations in springbok body condition. *J. Anim. Ecol.* 81, 58–69. <https://doi.org/10.1111/j.1365-2656.2011.01892.x>.
- Ullmann, T., Heinze, G., Hafermann, L., Schilhart-Wallisch, C., Dunkler, D., for TG2 of the STRATOS initiative, 2024. Evaluating variable selection methods for multivariable regression models: a simulation study protocol. *PLoS One* 19, e0308543. <https://doi.org/10.1371/journal.pone.0308543>.
- Van Vuure, T., 2002. *History, morphology and ecology of the aurochs*. *Lutra* 45.
- Van Wyk, J.A., Mayhew, E., 2013. Morphological identification of parasitic nematode infective larvae of small ruminants and cattle: a practical lab guide. *Onderstepoort J. Vet. Res.* 80, 1–14. <https://doi.org/10.4102/ojvr.v80i1.539>.
- Verocai, G.G., Chaudhry, U.N., Lejeune, M., 2020. Diagnostic methods for detecting internal parasites of livestock. *Vet. Clin. North Am. Food Anim. Pract.* 36, 125–143. <https://doi.org/10.1016/j.cvfa.2019.12.003>.
- Vicente, J., Höfle, U., Fernández-De-Mera, I.G., Gortazar, C., 2007. The importance of parasite life history and host density in predicting the impact of infections in red deer. *Oecologia* 152, 655–664. <https://doi.org/10.1007/s00442-007-0690-6>.
- Vuković, S., 2021. *The Story of a Vanished Creature: Extinction Dynamics of the Aurochs from the Territory of Present-Day Serbia*. *Archaeology Crisis*, pp. 221–238.
- Watwiengkam, N., Patikae, P., Thiangthientham, P., Ruksachat, N., Simkum, S., Arunlerk, K., Chooyoung, K., Purisotayo, T., 2024. Prevalence of gastrointestinal parasites in free-ranging bantengs (*Bos javanicus*) and domestic cattle at a wildlife and livestock interface in Thailand. *Trends Sci.* 21, 7368. <https://doi.org/10.48048/tis.2024.7368>.
- Weik, F., Archer, J.A., Morris, S.T., Garrick, D.J., Miller, S.P., Boyd, A.M., Cullen, N.G., Hickson, R.E., 2021. Live weight and body condition score of mixed-aged beef breeding cows on commercial hill country farms in New Zealand. *N. Z. J. Agric. Res.* 1–16. <https://doi.org/10.1080/00288233.2021.1901235>.
- Wong, L., Corlett, R.T., Young, L., Lee, J.S., 2001. Utilization of Wetlands by Ardeids in Starling Inlet, Hong Kong: a Year-Round Study and a Comparison between the Census and Flight-Line Methods. *Waterbirds*, pp. 153–160.
- Zeiss, C., 2024. *Labscope*.
- Zhang, Z., 2025. Free-roaming bovids in Hong Kong, worlding the more-than-human care. *Eur. J. Cult. Stud.* 13675494251322107. <https://doi.org/10.1177/13675494251322107>.
- Zuur, A.F., Ieno, E.N., 2016. *Beginner's Guide to Zero-Inflated Models with R*. Highland Statistics Ltd, Newburgh.