Intestinal parasites of endangered orangutans (*Pongo pygmaeus*) in Central and East Kalimantan, Borneo, Indonesia

E. M. LABES[1]*, D. HEGGLIN[1], F. GRIMM[1], W. NURCAHYO[2], M. E. HARRISON[3,4], M. L. BASTIAN[5] *and* P. DEPLAZES[1]

[1] *University of Zurich, Institute of Parasitology, Winterthurerstrasse 266a, 8057 Zurich, Switzerland*
[2] *Gadjah Mada University, Faculty of Veterinary Medicine, Laboratory of Parasitology, 55281 Yogyakarta, Indonesia*
[3] *University of Cambridge, The Anatomy School, Wildlife Research Group, Downing Street, Cambridge CB2 3DY, UK*
[4] *University of Palangka Raya, Centre for the International Cooperation in Management of Tropical Peatlands, Palangka Raya, Central Kalimantan, Indonesia*
[5] *Duke University, Department of Biological Anthropology and Anatomy, Science Drive, Box 90383, Durham, NC 27708-0383, USA*

(*Received 23 May 2009; revised 4 July 2009; accepted 7 July 2009; first published online 21 September 2009*)

SUMMARY

Faecal samples from 163 captive and semi-captive individuals, 61 samples from wild individuals and 38 samples from captive groups of Bornean orangutans (*Pongo pygmaeus*) in Kalimantan, Indonesia, were collected during one rainy season (November 2005–May 2006) and screened for intestinal parasites using sodium acetate-acetic acid-formalin-concentration (SAFC), sedimentation, flotation, McMaster- and Baermann techniques. We aimed to identify factors influencing infection risk for specific intestinal parasites in wild orangutans and individuals living in captivity. Various genera of Protozoa (including *Entamoeba, Endolimax, Iodamoeba*, *Balantidium*, *Giardia* and *Blastocystis*), nematodes (such as *Strongyloides*, *Trichuris*, *Ascaris, Enterobius*, *Trichostrongylus* and hookworms) and one trematode (a dicrocoeliid) were identified. For the first time, the cestode *Hymenolepis* was detected in orangutans. Highest prevalences were found for *Strongyloides* (individuals 37%; groups 58%), hookworms (41%; 58%), *Balantidium* (40%; 61%), *Entamoeba coli* (29%; 53%) and a trichostrongylid (13%; 32%). In re-introduction centres, infants were at higher risk of infection with *Strongyloides* than adults. Infection risk for hookworms was significantly higher in wild males compared with females. In groups, the centres themselves had a significant influence on the infection risk for *Balantidium*. Ranging patterns of wild orangutans, overcrowding in captivity and a shift of age composition in favour of immatures seemed to be the most likely factors leading to these results.

Key words: Bornean orangutan, *Pongo pygmaeus*, intestinal parasite, infection risk parameter.

INTRODUCTION

Orangutans belong to the family Pongidae and represent the only great ape in Asia. Wild populations are restricted to the islands of Borneo (*Pongo pygmaeus*) and Sumatra (*Pongo abelii*), in Indonesia and Malaysia (Rijksen and Meijaard, 1999). Currently, 3 subspecies of Bornean orangutans are recognized (*P. p. pygmaeus*, *P. p. wurmbii* and *P. p. morio*) (Xu and Arnason, 1996; Groves, 1999). In the last few decades, the total number and distribution of orangutans have reduced drastically, primarily as a result of habitat loss (Wich *et al*. 2008). In 1997, the population estimate for Bornean orangutans was only 7% of that in 1900 (Rijksen and Meijaard, 1999), and the species is now classified as endangered by the International Union for Conservation of Nature (IUCN, 2008).

Infectious diseases caused by parasites can pose a severe threat to great ape survival. Parasites can be transmitted between wild and rehabilitant populations, between both of these and other wildlife species, and between great apes and humans and/or their livestock (Hira and Patel, 1980; Ashford *et al*. 1990; Landsoud-Soukate *et al*. 1995; Michaud *et al*. 2003; Hope *et al*. 2004; Appelbee *et al*. 2005; Nunn and Altizer, 2006; Garber, 2008; Pusey *et al*. 2008). Since orangutans share ~96·4% of their genetic information with humans (see Miyamoto, 1988; Chen and Li, 2001), zoonotic diseases are of major significance. Certain viral diseases and parasite infections have already been well documented in African great apes (Eberle and Hilliard, 1989; Brooks *et al*. 2002; Grimm *et al*. 2003; Whitfield, 2003; Karesh and Reed, 2004; Graczyk *et al*. 1999, 2001, 2002; Sleeman *et al*. 2000; Freeman *et al*. 2004; Van Heuverswyn *et al*. 2006; Kaur *et al*. 2008; Williams

* Corresponding author: University of Zurich, Institute of Parasitology, Winterthurerstrasse 266a, 8057 Zurich, Switzerland. Tel: +41 (0)44 310 3210. Fax: +41 (0)44 310 3211. E-mail: elabes@bluewin.ch

Parasitology (2010), **137**, 123–135.
doi:10.1017/S0031182009991120 Printed in the United Kingdom

et al. 2008). Although the occurrence of various pathogenic gastrointestinal parasites has been described in captive, rehabilitant and wild orangutans (Cummins *et al*. 1973; Collet *et al*. 1986; Leeflang and Markham, 1986; Foitová *et al*. 2009), the distribution and transmission of parasites of orangutans are still poorly understood compared with African great apes.

Captive orangutans are often kept under unnatural conditions and in close contact with humans and/or other animal species, which allows pathogens to be readily transmitted from humans to orangutans (Chitwood, 1970; Ott-Joslin, 1993) and *vice versa*. Intestinal parasites that have already been described in orangutans (Rijksen, 1978; Collet *et al*. 1986; Wells *et al*. 1990; Djojosudharmo and Gibson, 1993; Warren, 2001; Kilbourn *et al*. 2003; Mul *et al*. 2007; Foitová *et al*. 2009) have also been identified in humans in Indonesia (Cross *et al*. 1975, 1976; Putrali *et al*. 1977; Joseph *et al*. 1978) and include various genera of Protozoa (*Entamoeba*, *Endolimax*, *Iodamoeba*, *Balantidium* and *Giardia*), nematodes (*Strongyloides*, *Ascaris*, *Enterobius*, *Trichuris* and hookworms), cestodes (*Hymenolepis*) and trematodes (dicrocoeliids). However, only few studies of orangutan health have been published in recent years (Warren, 2001; Kilbourn *et al*. 2003; Mul *et al*. 2007; Foitová *et al*. 2009), and most studies include only small numbers of free-ranging orangutans (see Rijksen, 1978; Collet *et al*. 1986; Djojosudharmo and Gibson, 1993; Warren, 2001; Mul *et al*. 2007), probably due to the difficulty of acquiring faecal samples from wild individuals. Furthermore, although transmission pathways of parasitic infections should differ between wild and captive populations, factors influencing the infection risk for specific parasites in wild populations compared with those living in captivity have not yet been elucidated.

Conservation efforts that focus on the health management of wild and captive orangutan populations should not only consider parasite prevalence, but also identify parameters that may increase infection risk and the anthropogenic influence on pathogen infections. Therefore, data from larger groups of wild individuals are needed, particularly since orangutans differ profoundly in their biology from African great apes (e.g., Knott, 2001, 2005; Yamagiwa, 2004).

In this study, wild Bornean orangutans from 3 distinct populations were compared with captive individuals and groups from 2 re-introduction centres. All sites were located in Kalimantan, Borneo. Differences in parasite prevalence were investigated with respect to ecological and behavioural factors as well as husbandry. The aim of the study was to identify factors that significantly influence the infection risk of individuals for specific parasites under different conditions. Gaining information in this context would provide a first step in understanding whether similar underlying factors influence infection risk in wild and captive orangutan populations, or whether these factors differ.

MATERIALS AND METHODS

Study site

Samples were collected at 2 re-introduction centres, both of which are managed by the Borneo Orangutan Survival Foundation (BOS), Indonesia. The Nyaru Menteng Orangutan Re-introduction Centre (centre 1) was founded in 1998 and is located 28 km north of Palangka Raya (2°21′56·27″S, 113°55′12·48″E), the capital of the province of Central Kalimantan. The centre covers 1·5 ha and neighbours the Nyaru Menteng Arboretum, a 62·5 ha lowland swamp forest. The Wanariset Orangutan Reintroduction Centre (centre 2) was founded in 1991 and is located 35 km north of Balikpapan (1°16′01·03″S, 116° 50′01·46″E), East Kalimantan. Centre 1 is regularly accessed by long-tailed macaques (*Macaca fascicularis*) and domestic dogs roaming for food. Domestic cats from the neighbourhood are often seen at both centres. Both centres occasionally receive other wild animals through confiscations, including Mueller's gibbons (*Hylobates muelleri muelleri*), proboscis monkeys (*Nasalis larvatus*), Bornean slow lorises (*Nycticebus menagensis*) and sun bears (*Helarctos malayanus*).

Faecal samples from free-ranging (wild) orangutans were collected from 3 geographically isolated populations at the Tuanan Research Station (site 1) in the Mawas area (2°09′06·1″S, 114° 26′26·3″E), the Sungai Lading Research Station (site 2), separated from the Mawas area by artificial water channels, and the Natural Laboratory of Peat Swamp Forest, Sabangau (2°19′40·72″S, 113°54′39·74″E) (site 3), a protected research area 20 km southwest of Palangka Raya. Orangutan density ranged from 4·25 to 4·5 individuals/km^2 in Tuanan (Van Schaik *et al*. 2005), 2·3 individuals/km^2 in Sabangau (Ley-Vela, 2005) and 7·74 individuals/km^2 at Sungai Lading (Bastian, 2008). All field sites are located in the province of Central Kalimantan and consist of disturbed peat-swamp forest habitat that had previously been subject to selective commercial and informal logging.

Subjects

Investigations at centre 1 were carried out between November 2005 and January 2006, during which time a total of 404 orangutans lived at the centre. Sample collection and analysis at centre 2 was carried out between March and May 2006, when the centre took care of a total of 191 orangutans. Individuals were either captive (confiscated) or semi-captive

Table 1. Number of investigated samples with respect to sex, age classes and group size

Sample (*n*)	Variable	Category	N (%)
Individuals in re-introduction centres (*n* = 163 samples)	Sex	Females	77 (47)
		Males	86 (53)
	Age group	Infants ⩽5years	69 (42)
		Subadults 6–8 years	30 (18)
		Adults >8 years	61 (37)
Individuals in field sites (*n* = 61 samples)	Sex	Females	24 (39)
		Males	37 (61)
	Age group	Infants/Adolescents ⩽7–9 years	7 (11)
		Subadults 10–14 years	4 (7)
		adults ⩾15 years	50 (82)
Groups in re-introduction centres (*n* = 38 samples)	Sex	Only females	10 (26)
		Only males	8 (21)
		Mixed sexes	20 (53)
	Group size	2 Individuals	17 (45)
		>2 Individuals*	21 (55)

* 3–24 individuals per group.

(wild-caught individuals, living in degraded forest fragments that had entered oil-palm or other plantations, from which they were rescued) and kept under the same husbandry conditions. Because of their different geographical locations, centre 1 had more orangutans of the subspecies *P. p. wurmbii*, whereas centre 2 had more *P. p. morio*. Both centres applied the same programme of rehabilitation, aiming to release the apes into protected forest habitat. The field sites were inhabited by 3 distinct populations of *P. p. wurmbii*. Samples from habituated individuals in field sites were collected over one wet season between November 2005 and April 2006.

Sample collection

A total of 567 faecal samples were collected from orangutans at both the re-introduction centres and the field sites. Between 1 and 4, or 1 and 9 samples, respectively, were collected per individual and group. The number of samples per individual and group depended on different factors; e.g., housing system and social rehabilitation programme in captive and semi-captive orangutans, and monitoring restrictions in wild individuals. To guarantee the same sensitivity for each subgroup of the multivariate analyses, we included only the first sample of each individual ($n = 224$) and group ($n = 61$). Therefore, all prevalences recorded herein must be considered as minimal prevalence rates.

The age of the individuals was estimated by experienced staff at the re-introduction centres and biologists at the field sites, respectively. However, young orangutans, in particular, develop at a different rate in re-introduction centres compared with those in the wild. Following Rijksen (1978), and in order to avoid incorrect age classifications, individuals in the re-introduction centres and in the field sites were divided into different age groups (Table 1). The age of 3 individuals was unknown (2%). Thirty-eight faecal samples from orangutans kept in groups (21 and 17 in centres 1 and 2) were collected as blind samples and analysed for intestinal parasites. These groups did not include orangutans that had been investigated individually.

Sample analysis

The cages in the centres were installed between 20 and 80 cm above the ground. Thus, faeces dropped down between the cage bars, and samples were collected from the ground before the cages were cleaned early in the morning. At the field sites, samples were collected immediately after defaecation. All samples were homogenized thoroughly and examined using different coproscopic techniques to ensure the detection of all parasite stages potentially present in the samples. For the detection of protozoa, the sodium acetate-acetic acid-formalin-concentration (SAFC) technique was applied using 1 g of each sample (Marti and Escher, 1990). Ziehl-Neelsen staining of a faecal smear was used additionally to identify *Cryptosporidium* spp. (Current, 1989). The Baermann-technique (Garcia and Bruckner, 1997; 10 g) and a combined sedimentation and flotation (Garcia and Bruckner, 1997) were used to detect helminth larvae and eggs (10 g). Egg counts were performed by a modified McMaster technique (Schmidt, 1971; 4 g). Parasites were identified microscopically on the basis of the morphological characteristics (size, shape, colour and contents) of eggs, cysts and larvae. An ocular micrometer was used to measure the sizes of parasite eggs, cysts and larvae. Identification was mainly made to the genus level, because specific identification was usually not possible.

Statistical analysis

To identify specific factors affecting infection risk of orangutans, multivariate logistic regression modelling was applied, which avoids the pitfalls of univariate analyses. For modelling of the prevalence of identified intestinal parasites in individuals, only parasites with an overall prevalence of $\geqslant 10\%$ were included in the analysis. The variables 'origin', 'age' and 'sex' were selected as the most promising, independent variables for the modelling procedure of each the reintroduction centres and the field sites. Although the majority of orangutans at centres 1 and 2 were either *P. p. wurmbii* or *P. p. morio*, respectively, it was not possible to classify each individual to the subspecies level with certainty, because of the possibility of hybrids. For this reason, the variable 'origin' primarily includes the geographical location of centres 1 and 2, but also considers the corresponding subspecies.

In order to distinguish infections that were most probably present before entry into the centre and those acquired after arrival, a distinction was made between orangutans depending on how long they had been at the centre before the first sample was collected (new arrivals within 1 week before sampling: $n=33$ [20%]; arrivals 8–21 days before sampling: $n=31$ [19%]; and arrivals >21 days before sampling: $n=132$ [81%], respectively. In addition, the variables 'group contact' (with or without tactile contact to neighbouring conspecifics) and 'captive status' (captive *vs.* semi-captive) were included for the reintroduction centres. For the field sites, the variable 'flanged' *versus* 'unflanged males' was included because the development of cheek pads is considered a dominance sign in adult male orangutans (Utami *et al.* 2002). Differences in hormonal profiles (flanged males have higher concentrations of testosterone) and specific costs incurred (higher energetic demands due to increased size and injuries from fights) may also lead to decreased immuno-competence in flanged males (Maggioncalda *et al.* 1999) and, thus might relate to their susceptibility to parasitic infections. This variable was not considered for captive male orangutans, because its effect in situations in which individuals are caged is difficult to measure and the sample size in the study was too small. Finally, the variable 'mother' *versus* 'non-mother' was considered for females. For the groups, only the variables 'origin', 'captive status', 'group contact' and 'group size' were included in the analysis. The variable 'group size' included the absolute number of individuals per group.

Logistic regression models were calculated for each selected parasite individually. Models were fitted using all possible combinations of the selected predictor variables, but only models that significantly explained variation in the data set (log-likelihood ratio test) were considered for the model-selection process. Best models were selected using Akaike's information criterion (AIC, Akaike, 1973; Burnham and Anderson, 1998) corrected for small sample sizes (AICc). The model with the lowest AICc was considered the most parsimonious and only models with $\Delta\text{AICc}<2$ compared to the model with the lowest AICc were selected. Akaike model weights were calculated (Burnham and Anderson, 1998) to determine the degree to which a model was supported by the data. By definition, weights of selected models sum to 1, and higher weights indicate better explanatory power. To evaluate the relative importance of each explanatory variable, the AICc weights were summed over all models where that variable was present. A variable sums to 1 when it is included in all selected models, whereas a variable present in just one model is assigned the value of the corresponding model. The variables were then ranked according to the resulting AICc weight sums. Finally, effect sizes of parameters of the selected models were calculated using model averaging: parameter estimates are multiplied by the weight of the particular model and summed over all selected models containing the particular parameter to give the weighted average of parameter estimates (Johnson and Omland, 2004). Standard errors were calculated for parameter estimates following Burnham and Anderson (1998). Parameter estimate and $1{\cdot}96*$standard errors were exponentially transformed to express odds ratios and their 95% confidence intervals. An event is equally likely in both groups when the odds ratio is 1. Odds ratios with 95%-CI's that include 1 were not interpreted. Statistical analyses were performed using SPSS 13.0 (Norusis, 1986). The fit of the logistic regression models were tested by likelihood ratio tests. Maximal P values for the likelihood ratio tests are given for the selected models.

RESULTS

A total of 163 faecal samples from the 2 reintroduction centres (centre 1; 118 samples, centre 2; 45 samples) and 61 wild individuals (sites 1–3; 34, 14 samples and 13, respectively) were examined. Cysts and trophozoites of 6 genera of Protozoa, as well as eggs and larvae of various nematodes were identified (Table 2). In individuals, 3 genera of Protozoa, as well as *Strongyloides* sp., hookworms and a trichostrongylid nematode had prevalence rates of $\geqslant 10\%$. Subsequently, parasites whose prevalence was $\geqslant 10\%$ were included in the modelling procedure. Eggs from hookworms measured $62{\cdot}0 \pm 2{\cdot}0 \times 37{\cdot}7 \pm 2{\cdot}5\ \mu$m and were not identified to genus-level. Other strongylid eggs, measuring $74{\cdot}4 \pm 3{\cdot}6 \times 45{\cdot}8 \pm 4{\cdot}0\ \mu$m in size, tapered at one end, thin-shelled and colourless, were consistent with *Trichostrongylus* (and thus termed

Table 2. Prevalence of parasites identified in faecal samples from individuals at re-introduction centres and field sites

	Captive ($n=119$ samples) (%)	95% CI	Semi-captive ($n=44$ samples) (%)	95% CI	Total centres ($n=163$ samples) (%)	95% CI	Sites ($n=61$ samples) (%)	95% CI
NON-PATHOGENIC PROTOZOA								
Blastocystis sp.	15	9·2–22·8	14	5·1–27·4	15	9·7–21·1	11	4·7–22·2
Entamoeba coli	22	14·8–30·4	32	18·6–47·6	25	18·1–31·9	43	30·0–55·9
Entamoeba hartmanni	6	2·4–11·7	9	2·5–21·7	7	3·4–11·8	15	7·0–26·2
Endolimax nana	9	4·7–15·9	7	1·4–18·7	9	4·8–14·0	3	0·4–11·3
Iodamoeba buetschlii	4	1·4–9·5	7	1·4–18·7	5	2·1–9·4	2	0·0–8·8
FACULTATIVELY PATHOGENIC PROTOZOA								
Balantidium sp.	39	29·9–48·0	41	28·3–59	40	32·3–47·8	41	28·6–54·3
POTENTIALLY PATHOGENIC PROTOZOA								
Entamoeba histolytica/ E. dispar	3	0·9–8·4	35	0·1–12	3	1·0–7·0	28	17·1–40·8
Entamoeba spp.	12	6·6–19	6	8·2–32·7	13	8·7–19·7	16	8·2–28·1
Giardia sp.	3	0·9–8·4	0	0·6–15·5	4	1·4–7·8	3	0·4–11·3
HELMINTHS								
Strongyloides sp.	39	30·7–48·9	34	20·5–49·9	38	30·6–46·0	33	21·3–46·0
Hookworm	31	22·9–40·2	43	28·3–59	34	27·1–42·2	59	45·7–71·4
'*Trichostrongylus*-like' nematodes	3	0·9–8·4	25	13·2–40·3	9	5·2–14·7	21	11·9–33·7
Trichuris sp.	7	2·9–12·8	14	5·2–27·4	9	4·8–14·0	7	1·8–15·9
Ascaris sp.	1	0–4·6	0	0–8	1	0·0–3·4	0	0·0–5·9
Enterobius sp.	1	0–4·6	2	0·1–12	1	0·1–4·4	15	7·0–26·2
Dicrocoelium sp.	0	0–3·1	0	0–8	0	0·0–2·2	0	0·0–5·9
Hymenolepis sp.	0	0–3·1	0	0–8	0	0·0–2·2	3	0·4–11·3

''*Trichostrongylus*-like''). The germinal mass did not fill the shell of the eggs.

The samples of 5 individuals contained *Dicrocoelium*-like eggs. The eggs were $43 \pm 2{\cdot}4 \times 27{\cdot}8 \pm 2{\cdot}1$ μm in size and had a thick, brown shell, possessing an inconspicuous operculum and a miracidium. The individuals included 3 female and 1 male semi-captive orangutans at centre 1 and 1 captive male at centre 2. Two males and 1 female infant at the Tuanan Research Station tested positive for *Hymenolepis*. Eggs were $66 \pm 6{\cdot}3$ μm in diameter, subspherical, with a firm egg shell and a brown-coloured hue. The eggs lacked polar filaments and contained a hexacanth embryo.

Overall prevalence of intestinal parasites in samples from orangutans housed in groups was much higher than in those housed individually (Table 3). The range of identified parasites did not generally differ between groups and individuals. *E. coli*, *E. histolytica/dispar*, *Balantidium* sp., *Strongyloides* sp., hookworms and *Trichostrongylus*-like nematodes had significantly higher prevalences in samples collected from orangutans kept in groups than in individually-housed orangutans and were subsequently selected for the statistical analysis. Only 33 (20·3%) samples from individuals at the centres, the sample from 1 group (2·6%) and 6 (9·8%) samples from wild orangutans tested negative for parasites. All other samples tested positive for between 1 and 9 intestinal parasite species.

Except for 6 samples, all collected at centre 1, the number of helminth eggs identified in individuals was always <50 eggs/g (epg) faeces. Higher egg counts were recorded for 2 males $\leqslant 5$ years of age with tactile contact to conspecifics (*Trichuris* sp.: 300 epg, *Strongyloides* sp.: 50 epg), 1 female of the same age group but without tactile contact (*Strongyloides* sp.: 10 700 epg, hookworms: 13 350 epg, *Trichostrongylus*-like nematodes: 400 epg, *Trichuris* sp.: 150 epg) and one 6 to 8-year-old male without tactile contact (*Strongyloides* sp.: 1100 epg). The samples of two >8-year-old males without tactile contact to conspecifics had higher egg counts for 3 (*Strongyloides* sp.: 50 epg, hookworms: 600 epg, *Trichostrongylus*-like nematodes: 650 epg) and 2 helminths (*Strongyloides* sp.: 750 epg, hookworms: 250 epg), respectively. All samples from groups contained <50 epg with the exception of 1 sample with 1050 epg for *Strongyloides* sp. and 500 epg for hookworms, and 1 sample with 100 epg for *Trichuris* sp., both from centre 1.

The model selection procedure revealed significant models for several parasites (individuals in re-introduction centres: *Balantidium* sp., *Strongyloides* sp., hookworm; groups in re-introduction centres: *Balantidium* sp., hookworm, *Trichostrongylus*-like

Table 3. Prevalence of parasites identified in faecal samples from groups at re-introduction centres

	Centre 1 ($n=21$ samples) (%)	95% CI	Centre 2 ($n=17$ samples) (%)	95% CI	Total centres ($n=38$ samples) (%)	95% CI
NON-PATHOGENIC PROTOZOA						
Blastocystis sp.	14	3·0–36·3	12	1·5–36·4	13	4·4–28·1%
Entamoeba coli	52	29·8–74·3	53	27·8–77·0	53	35·8–69·0
Entamoeba hartmanni	10	1·2–30·4	18	3·8–43·4	13	4·4–28·1
Endolimax nana	10	1·2–30·4	24	6·8–49·9	16	6·0–31·3
Iodamoeba buetschlii	5	0·1–23·8	18	3·8–43·4	11	2·9–24·8
FACULTATIVELY PATHOGENIC PROTOZOA						
Balantidium sp.	76	52·8–91·8	41	18·4–67·1	61	43·4–76·0
POTENTIALLY PATHOGENIC PROTOZOA						
Entamoeba histolytica/E. dispar	43	21·8–66·0	35	14·2–61·7	39	24·0–56·6
Entamoeba spp.	14	3·0–36·3	6	0·1–28·7	11	2·9–24·8
Giardia sp.	0	0·0–16·1	0	0·0–19·5	0	0·0–9·3
HELMINTHS						
Strongyloides sp.	62	38·4–81·9	53	27·8–77·0	58	40·8–73·7
Hookworm	76	52·8–91·8	35	14·2–61·7	58	40·8–73·7
'*Trichostrongylus*-like' nematodes	52	29·8–74·3	6	0·1–28·7	32	17·5–48·7
Trichuris sp.	19	5·4–41·9	0	0·0–19·5	11	2·9–24·8
Ascaris sp.	0	0·0–16·1	0	0·0–19·5	0	0·0–9·3
Enterobius sp.	0	0·0–16·1	0	0·0–19·5	0	0·0–9·3
Dicrocoelium sp.	0	0·0–16·1	0	0·0–19·5	0	0·0–9·3
Hymenolepis sp.	0	0·0–16·1	0	0·0–19·5	0	0·0–9·3

nematodes; wild individuals: *Entamoeba* spp., hookworm). For these parasites, several models with similar explanatory power were selected (ΔAICc <2; Tables 4 and 5).

The averaged models comprised all factors that were added to the model-selection procedure. With 2 exceptions, the 95% CI for all odds ratios included 1 and were therefore not discussed. In individuals, only age for *Strongyloides* sp. at the centres and gender for hookworms at the field sites were found to be significant (Tables 6 and 7). Total prevalence for individuals $\leqslant 5$ years was 53·6% (95% CI 41·2–65·7), 6–8 years 26·7% (95% CI 12·3–45·9) and >8 years 27·9% (95% CI 17·1–40·8). Wild males had an overall prevalence of 73% (95% CI 55·9–86·2) and females of 38% (95% CI 18·8–59·4). There was no significant difference between the 3 field sites. In groups, only 'origin' for *Balantidium* sp. yielded a significant result in that the infection risk was higher in centre 1 than in centre 2 (Table 6).

DISCUSSION

Our analysis yielded 3 significant results, 1 for the field sites and 2 for the re-introduction centres. For the field sites, the ranking of the variables according to the AICc weight sums resulted in a significantly higher infection risk for hookworms in wild males than in females. No significant difference was found between flanged and unflanged males, indicating that the rank status does not influence infection risk in Bornean males. In humans, hookworms include *Ancylostoma duodenale* and *Necator americanus*, which produce eggs that cannot be distinguished morphologically (Muller, 2002). Hookworms are geohelminths, transmitted through oral, percutaneous and/or transmammary pathways. Mul *et al.* (2007) found a significantly higher total prevalence for intestinal parasites in wild females than in males, and interpreted this to be a result of females and their offspring having more frequent physical contact with conspecifics, compared with males. The percentage of wild individuals infected with *Strongyloides*, another soil transmitted nematode, was 33% in this study and 47% in the study by Mul *et al.* (2007). Parameters such as the level of arboreality or terrestriality influence parasite occurrence and prevalence in wild animal populations (Loehle, 1995; Vitone *et al.* 2004). Male Bornean orangutans are less territorial than females and frequently forage and travel over long distances on the ground, whereas this behaviour is rare for Sumatran orangutans (Delgado and Van Schaik, 2000). Male home ranges are also much larger than those of females (Singleton and Van Schaik, 2001; Setia *et al.* 2009), probably 3–5 times the size of female ranges, which are estimated to vary between 250 and 600 ha for *P. p. wurmbii* (see Utami Atmoko *et al.* 2009*a*). As a result, males will come into contact with both a greater number and more distant individuals than females. Therefore, males have more occasions for direct contact with soil and faeces from other orangutans, animal species and

Table 4. Results from logistic-regression model selection to explain prevalence rates of *Balantidium* sp., *Strongyloides* sp. and hookworm in Bornean orangutans at re-introduction centres (individuals: $n=163$; groups: $n=38$)

Model		AICc	ΔAICc	AICc weights
		Individuals		
(a)	*Balantidium* sp.			
	Origin, new arrivals	47·74	0·00	0·25
	Origin, arrivals	48·33	0·59	0·19
	Origin, sex, new arrivals	48·76	1·02	0·15
	New arrivals	48·81	1·06	0·15
	Arrivals	48·97	1·23	0·14
	Origin, arrivals, sex	49·30	1·56	0·12
(b)	*Strongyloides* sp.			
	Origin, age	40·84	0·00	0·29
	Origin, age, sex	41·65	0·82	0·20
	Age	42·20	1·36	0·15
	Origin, arrivals, age	42·42	1·58	0·13
	Origin, age, captive status	42·67	1·84	0·12
	Origin, age, new arrivals	42·78	1·95	0·11
(c)	Hookworm			
	Origin, sex, new arrivals	38·97	0·00	0·13
	Origin, arrivals, sex	39·06	0·09	0·13
	Origin, new arrivals	39·29	0·32	0·11
	Origin, arrivals	39·32	0·34	0·11
	Sex, new arrivals	39·86	0·89	0·09
	New arrivals	39·95	0·97	0·08
	Arrivals	40·43	1·45	0·06
	Arrivals, sex	40·48	1·50	0·06
	Captive status, sex, new arrivals	40·76	1·79	0·05
	Origin, captive status, sex, new arrivals	40·79	1·82	0·05
	Origin, arrivals, captive status, sex	40·83	1·86	0·05
	Captive status, new arrivals	40·85	1·88	0·05
		Groups		
(a)	*Balantidium* sp.			
	Origin	14·04	0·00	0·56
	Origin, group contact*	14·56	0·52	0·44
(c)	Hookworm			
	Origin	13·24	0·00	0·60
	Captive status	14·02	0·78	0·40
(d)	'*Trichostrongylus*-like' nematodes			
	Origin, group contact*, number of individuals°	−2·20	0·00	1·00

* Group contact = without tactile contact *vs* with tactile contact.
° Number of individuals = number of individuals per group.

Table 5. Results from logistic-regression model selection to explain prevalence rates of *Entamoeba* spp. and hookworm in Bornean orangutans at field sites ($n=61$)

Model		AICc	ΔAICc	AICc weights
(a)	*Entamoeba* spp.			
	Age, flanged	−5·15	0·00	0·64
	Age	−4·01	0·57	0·36
(b)	Hookworm			
	Sex	20·46	0·00	0·67
	Origin, sex	21·87	1·41	0·33

humans, and may play an important role in the transmission of pathogens to other orangutans (and wildlife species) over large areas. For soil-transmitted nematodes, these males may be suitable distributors. Since Bornean males have more contact with females than male competitors (Van Schaik, 1999), infections are probably most frequently passed from males to these females and subsequently to their infants. Dominant males and receptive females can travel together for days or even up to months (Utami Atmoko *et al*. 2009*b*). Sumatran orangutans almost never leave the trees, probably because of terrestrial predators in their habitat (Delgado and Van Schaik, 2000; Van Schaik, 1999), but form larger temporary

Table 6. Odds ratios (OR) and 95% confidence intervals (CI) for the averaged models for individuals and groups at re-introduction centres

Model	OR	95% CI
	Individuals	
(a) *Balantidium* sp.		
Arrivals	0·56	0·14–2·27
New arrivals	2·24	0·45–11·12
Origin (centre 1 *vs* centre 2)	1·69	0·68–4·2
Sex	0·9	0·61–1·32
(b) *Strongyloides* sp.		
Origin	2·11	0·79–5·69
Age (⩽5 yrs *vs* >8 yrs)	**3·05**	**1·39–6·73**
Age (⩽8 yrs *vs* >8 yrs)	1·21	0·43–3·37
Captive status	1·03	0·87–1·23
New arrivals	0·97	0·83–1·14
Sex	1·1	0·79–1·52
Arrivals	1·1	0·83–1·33
(c) Hookworm		
Origin	1·61	0·59–4·39
Sex	0·72	0·34–1·53
New arrivals	0·53	0·15–1·84
Arrivals	1·53	0·52–4·5
Captive status	0·93	0·67–1·28
	Groups	
(a) *Balantidium* sp.		
Origin (centre 1 *vs* centre 2)	**5·81**	**1·14–29·54**
Group contact*	0·58	0·12–2·79
(c) Hookworm		
Origin	2·87	0·38–21·67
Captive status (heterogeneous *vs* semi-captive)	2373·38	0·00– (—)
Captive status (captive *vs* semi-captive)	0·42	0·04–4·53
(d) '*Trichostrongylus*-like' nematodes		
Origin	(—)	0·00–(—)
Group contact*	0·00	0·00–(—)
Number of individuals°	0·00	0·00–(—)

* Group contact = without tactile contact *vs* with tactile contact.
° Number of individuals = number of individuals per group.

Table 7. Odds ratios (OR) and 95% confidence intervals (CI) for the averaged models for individuals at field sites

Model	OR	95% CI
(a) *Entamoeba* spp.		
Age	5·27	0·25–111·16
Flanged	0·24	0·01–3·95
(b) *Hookworm*		
Sex (males *vs* females)	**4·38**	**1·37–14·06**
Origin	0·86	0·42–1·74

groups in which all individuals, and especially infants, have more tactile contact with each other (Delgado and Van Schaik, 2000). In this study, no significant difference was found between females with or without offspring, indicating that offspring does not increase infection risk in females. Bornean orangutans only form small temporary social units of 2 or 3 individuals (Delgado and Van Schaik, 2000; Harrison, 2009), and females spend much less time in associations than Sumatran females (Van Schaik, 1999; Wich *et al*. 1999). Infection risk in these units may be lower for a soil-transmitted nematode than in larger groups.

However, from the perspective of disease risk, spatial isolation could be viewed as an adaptive strategy of the primate host to avoid soil-transmitted parasites. Spatial isolation of social groups or individuals is known to be an effective strategy in preventing transmission or attack of pathogens (Loehle, 1995). The different results of Mul *et al*. (2007) and this study therefore indicate that the level of arboreality and ranging patterns of this ape may be linked to avoidance of faecal-contaminated pathways, as suggested by Freeland (1980) for Mangabeys (*Cercocebus albigena*). Thus, in addition to the predator hypothesis mentioned above, these results may also represent a link between orangutan socioecology and disease risk, reflecting the consequences of variation in the social structure of these two orangutan species for infection risk from at least one important nematode group.

To our knowledge, this is the first record of *Hymenolepis* eggs in the faeces from orangutans. Eggs of these cestode species were found in 2 male and 1 female orangutans from the Tuanan site. The eggs were morphologically indistinguishable from eggs of *H. diminuta* which is widely distributed in rats, with arthropods serving as intermediate hosts. No proglottids of *Hymenolepis* sp. were found in the faeces. Similarly, eggs of a dicrocoeliid were found in 5 orangutans, 4 of which were rescued from oil-palm plantations. The eggs morphologically resembled those of *D. dendriticum*. The genus *Dicrocoelium* has been described previously in Bornean orangutans (Collet *et al*. 1986; Djojosudharmo and Gibson, 1993). Its life cycle includes ants as intermediate hosts and mammals, including humans, as final hosts. In this study, the infected individuals most probably acquired the eggs of both genera through accidental ingestion of infected invertebrate hosts, which are frequently consumed by orangutans in peat swamps (e.g. Harrison, 2009). However, to what extent both parasites may be infectious to orangutans, giving the ape a role in the parasites' life cycle, can neither be inferred from the findings of this nor from previous studies (see Collet *et al*. 1986; Djojosudharmo and Gibson, 1993).

The ranking of the variables according to the AICc weight sums resulted in 2 significant differences for the re-introduction centres. Whereas age had the

strongest influence on infection risk for *Strongyloides* in individuals, the centres themselves significantly influenced the infection risk for *Balantidium* in captive groups. In individuals, infants $\leqslant 5$ years of age had a significantly higher risk of infection with *Strongyloides* than orangutans >8 years. The reproductive cycle of *Strongyloides* sp. is almost unique among nematode parasites of vertebrates, in that it includes a free-living adult generation, which mates to produce eggs and progeny (Viney and Lok, 2007). Tropical climate conditions favour sexual reproduction and thereby provide a relatively high number of infective larvae for host invasion. Infected young individuals in captivity easily pass the infection to group members. Prevalence in young individuals is generally typically higher than in adults (Viney and Lok, 2007), with captive infant and juvenile orangutans being particularly susceptible to developing hyperinfection and strongyloidosis (Cummins *et al*. 1973; Wells *et al*. 1990). This high susceptibility in comparison to other great apes may have an immunological basis, because arboreal orangutans in the wild have fewer occasions to acquire an infection (Harper *et al*. 1982). With 42% of all orangutans kept at the two centres being $\leqslant 5$ years of age, the age composition in the centres resulted in a shift towards a higher percentage of immature individuals compared to natural conditions. Captive situations can afford to keep young individuals in groups and on the ground, meaning that the adaptive strategies of the species to prevent infection cannot come to effect. In contrast, age does not seem to have a significant influence on the prevalence of *Strongyloides* sp. in wild orangutans (see Foitová *et al*. 2009). Furthermore, in an internal survey carried out by centre 1, only 3 of 15 examined caretakers tested negative and the identified parasites were identical to those found in the orangutans. Infant orangutans regularly defecated onto the centre's lawn and other grounds. The caretakers had daily physical contact with about 60 infant orangutans, but did not wear any protective clothing (boots, gloves), allowing intestinal parasites to be transferred back and forth between orangutans and staff. The animals and their environment on one side, and the human caretakers on the other, may therefore represent a relevant source of infection for each other. The potential risk of contact with humans on parasite prevalence in nonhuman primates has also been described by other authors (for an overview see Foitová *et al*. 2009). Prevalence for *Strongyloides* sp. was also higher in captive compared to wild orangutans in other studies, although the difference was not significant (see Warren, 2001; Mul *et al*. 2007). The results of this study clearly indicate an anthropogenic influence on parasite prevalence, bolstered by unnatural husbandry conditions (shift of age composition, dense groups, time spent on the ground), and supports the contention that in communities comprised of closely related species, cross-species interaction may be an important source of infection (Ezenwa, 2003).

The infection risk for *Balantidium* sp. was significantly higher in centre 1 than centre 2. *Balantidium sp*. is the only facultative pathogenic ciliate. *B. coli* are widely distributed in monkeys in the tropics (Garcia and Bruckner, 1997) which are considered a reservoir for humans. Under humid conditions, *B. coli* cysts can stay infectious for weeks and therefore survive for a long time within a host population. In this study, 16 (76%) of 21 groups at centre 1 tested positive for *Balantidium* sp., of which 13 also tested positive for *Strongyloides* sp., hookworms and/or *Trichostrongylus*-like nematodes. *Balantidium* sp. may have functioned as a secondary infection, although no correlation with signs of diarrhoea was found. Highest prevalence for *Balantidium* sp. in the centres was found in groups of >2 animals with tactile contact to conspecifics outside of their group and/or access to a neighbouring forest, staying at the centre for >21 days, and in groups consisting of mothers with their infants. Captive groups can easily be infected through various sources, including newly-arriving individuals, contaminated food or water, insects, and other primates or animal species in the forest. In combination with the physical contact between the infected groups, which were of young age, this most probably contributed to the result for centre 1. In addition, this centre took care of 7 semi-captive mothers with their infants, of which 5 tested positive for *Balantidium* sp. Being rescued from plantations and protecting their offspring while in captivity, these mothers were constantly susceptible to stress and subsequently to infections with this parasite. The synergistic relationship between stress and *Balantidium* infections has been shown in several studies (Anargyrou *et al*. 2003; Ho-Seong *et al*. 2006). A study on red colobus by Chapman *et al*. (2006) supports the hypothesis that stress weakens the immune system and leads to a higher prevalence of parasite infection. Host density positively correlates with parasite prevalence and diversity (Packer *et al*. 1999), not only in the field, and host density is positively linked to the spread of directly transmitted parasites (Arneberg, 2002). The unnatural density of the investigated groups and possible rank competition in those with older individuals should have increased the stress level of the group members, thereby increasing their susceptibility to infection.

In the present study, we examined specific parameters that influence infection risk for intestinal parasites in wild and captive orangutans. Our results have relevance for conservation and management plans for Bornean orangutans, as well as Indonesian public health programmes. Further investigations of factors, such as life history, social contact, range-use intensity, diet and habitat diversity on infectious disease dynamics, are needed in order to better

understand the influence of these factors in reducing or increasing infection risk from intestinal parasites in orangutan populations. Molecular tools should assist in conducting future epidemiological investigations of the parasites.

ACKNOWLEDGEMENTS

We would like to thank the Indonesian Institute of Science (LIPI) and the Indonesian Nature Conservation Service (PHKA) for permission to work in Indonesia. We thank the Borneo Orangutan Survival Foundation in Indonesia for their support and the permission to work in their reintroduction centres. We also thank the field staff at the Tuanan Research Station, the Natural Laboratory of Peat Swamp Forest, Sabangau, and the Sungai Lading Research Station as well as the staff of BOS' two reintroduction centres Nyaru Menteng and Wanariset for their assistance. We thank the Laboratory of Parasitology, University Gadjah Mada, for offering their facilities. We also acknowledge the Centre for the International Cooperation in Management of Tropical Peatlands for permission to work in Sabangau and are thankful to Helen Morrogh-Bernard and Suwido Limin for their support. This work was supported by a grant from the Messerli Foundation, Switzerland.

REFERENCES

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory, Tsahkadsor, Armenian SSR* (ed. Petrov, B. N. and Csaki, F.), pp. 267–281. Akademiai Kiado, Budapest, Hungary.

Anargyrou, K., Petrikkos, G. L., Suller, M. T. E., Skiada, A., Siakantaris, M. P., Osuntoyinbo, R. T., Pangalis, G. and Vaiopoulos, G. (2003). Pulmonary *Balantidium coli* infection in a leukemic patient. *American Journal of Hematology* **73**, 180–183.

Appelbee, A. J., Thompson, R. C. A. and Olson, M. E. (2005). *Giardia* and *Cryptosporidium* in mammalian wildlife – current status and future needs. *Trends in Parasitology* **21**, 370–376.

Arneberg, P. (2002). Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**, 88–94.

Ashford, R. W., Reid, G. D. F. and Butynski, T. M. (1990). The intestinal faunas of man and mountain gorillas in a shared habitat. *Annals of Tropical Medicine and Parasitology* **84**, 337–340.

Bastian, M. L. (2008). Effects of a riverine dispersal barrier on cultural similarity in wild *Bornean orangutans* (*Pongo pygmaeus wurmbii*). Ph.D. dissertation, Duke University, Durham, NC, USA.

Brooks, J. I., Rud, E. W., Pilon, R. G., Smith, J. M., Switzer, W. M. and Sandstrom, P. A. (2002). Cross-species retroviral transmission from macaques to human beings. *Lancet* **260**, 387–388.

Burnham, K. and Anderson, D. (1998). *Model Selection and Inference: A Practical Information-theoretic Approach*. Springer, New York, USA.

Chapman, C. A., Wasserman, M. D., Gillespie, T. R., Speirs, M. L., Lawes, M. J., Saj, T. L. and Ziegler, T. E. (2006). Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology* **131**, 525–534.

Chen, F. C. and Li, W. H. (2001). Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. *American Journal of Human Genetics* **68**, 444–456.

Chitwood, M. (1970). Comparative relationships of some parasites of man and old and new world subhuman primates. *Laboratory Animal Care* **20**, 389–394.

Collet, J. Y., Galdikas, B. M. F., Sugarjito, J. and Jojosudharmo, S. (1986). A coprological study of parasitism in orangutans (*Pongo pygmaeus*) in Indonesia. *Journal of Medical Primatology* **15**, 121–129.

Cross, J. H., Clarke, M. D., Cole, W. C., Lien, J. C., Partono, F., Djakaria, Joesoef, A. and Oemijati, S. (1976). Parasitic infections in humans in West Kalimantan (Borneo), Indonesia. *Tropical Geographical Medicine* **28**, 121–130.

Cross, J. H., Clarke, M. D., Durfee, P. T., Irving, G. S., Taylor, J., Partono, F., Joesoef, A., Hudojo and Oemijati, S. (1975). Parasitology survey and seroepidemiology of amoebiasis in South Kalimantan (Borneo), Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health* **6**, 52–60.

Cummins, L. B., Keeling, M. E. and McClure, H. M. (1973). Preventative medicine in anthropoids: parasite control. *Laboratory Animal Science* **23**, 819–822.

Current, W. L. (1989). Cryptosporidiosis. In *New Strategies in Parasitology* (ed. McAdam, K. P. W. J.), pp. 257–273. Livingstone, Edinburgh, UK.

Delgado, R. A. and Van Schaik, C. P. (2000). The behavioural ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. *Evolutionary Anthropology* **9**, 201–218.

Djojosudharmo, S. and Gibson, A. T. (1993). Parasit intestinalis pada primat liar di Taman Nasional Gunung Leuser, Sumatra. In *Simposium and Seminar Nasional Primata*, Bandung, Sumatra. pp. 13–14.

Eberle, R. and Hilliard, J. K. (1989). Serological evidence for variation in the incidence of herpesvirus infections in different species of apes. *Journal of Clinical Microbiology* **27**, 1357–1366.

Ezenwa, V. O. (2003). Habitat overlap and gastrointestinal parasitism in sympatric African bovids. *Parasitology* **126**, 379–388.

Foitová, I., Huffman, M. A., Wisnu, N. and Olsansky, M. (2009). Parasites and their impacts on orangutan health. In *Orangutans – Geographic Variation in Behavioral Ecology and Conservation* (ed. Wich, S. A., Utami Atmoko, S. S., Setia, T. M. and Van Schaik, C. P.), pp. 157–169. Oxford University Press, Oxford, UK.

Freeland, W. J. (1980). Mangabey (*Cercocebus albigena*) movement patterns in relation to food availability and faecal contamination. *Ecology* **61**, 1297–1303.

Freeman, A. S., Kinsella, J. M., Cipolletta, C., Deem, S. L. and Karesh, W. B. (2004). Endoparasites of Western Lowland Gorillas (*Gorilla gorilla gorilla*) at Bai

Hokou, Central African Republic. *Journal of Wildlife Diseases* **40**, 775–781.

Garber, P. A. (2008). Disease transmission from humans to wild apes: perspectives on the costs and benefits of research and conservation. *American Journal of Primatology* **70**, 715.

Garcia, L. S. and Bruckner, D. A. (1997). *Diagnostic Medical Parasitology*, 3rd. edn. ASM Press, Washington, USA.

Graczyk, T. K., Bosco-Nizeyi, J., Ssebide, B., Thompson, R. C., Read, C. and Cranfield, M. R. (2002). Anthropozoonotic *Giardia duodenalis* genotype (assemblage) infections in habitats of free-ranging human-habituated gorillas, Uganda. *Journal of Parasitolgy* **88**, 905–909.

Graczyk, T. K., DaSilva, A. J., Cranfield, M. R., Nizeyi, J. B., Kalema, G. R. and Pieniazek, N. J. (2001). *Cryptosporidium parvum* genotype 2 infections in free-ranging mountain gorillas (*Gorilla gorilla beringei*) of the Bwindi Impenetrable National Park, Uganda. *Parasitology Research* **87**, 368–370.

Graczyk, T. K., Lowenstine, L. J. and Cranfield, M. R. (1999). *Capillaria hepatica* (Nematoda) infections in human-habituated mountain gorillas (*Gorilla gorilla beringei*) of the Parc National de Volcans, Rwanda. *Journal of Parasitology* **85**, 1168–1170.

Grimm, T. A., Beer, B. E., Hirsch, V. M. and Clouse, K. A. (2003). Simian immunodeficiency viruses from multiple lineages infect human macrophages: implications for cross-species transmission. *Journal of Acquired Immune Deficiency Syndromes* **32**, 362–369.

Groves, C. P. (1999). The taxonomy of orang-utans. In *Orangutan Action Plan* (ed. Yeager, C.), pp. 27–30. WWF, Jakarta, Indonesia.

Harper, J., Rice, J. M., London, W. T., Sly, D. L. and Middleton, C. (1982). Disseminated strongyloidosis in *Erythrocebus patas*. *American Journal of Primatology* **3**, 89–98.

Harrison, M. E. (2009). Orang-utan feeding behaviour in Sabangau, Central Kalimantan. Ph.D. dissertation, University of Cambridge, Cambridge, UK.

Hira, P. R. and Patel, B. G. (1980). Human strongyloidiasis due to the primate species *Strongyloides fülleborni*. *Tropical and Geographical Medicine* **32**, 23–29.

Hope, K., Goldsmith, M. L. and Graczyk, T. (2004). Parasitic health of olive baboons in Bwindi Impenetrable National Park, Uganda. *Veterinary Parasitology* **122**, 165–170.

Ho-Seong, C., Sung-Shik, S. and Nam-Yong, P. (2006). Balantidiasis in the gastric lymph nodes of Barbary sheep (*Ammotragus lervia*): an incidental finding. *Journal of Veterinary Science* **7**, 207–209.

IUCN (2008). *IUCN Red List of Threatened Species*. www.redlist.org

Johnson, J. B. and Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19**, 101–108.

Joseph, S. W., Carney, W. P., Van Peenen, P. F., Russell, D. and Saroso, J. S. (1978). Human parasitosis of the Malili area, South Sulawesi (Celebes) province, Indonesia. *Southeast Asian Journal of Tropical Medicine and Public Health* **9**, 264–271.

Karesh, W. B. and Reed, P. (2004). Population health concerns for lowland gorillas and other great apes. *Diseases – the Third Major Threat for Wild Great Apes? Max Planck Institute for Evolutionary Anthropology*, Leipzig, Germany 6–9 May, 2004.

Kaur, T., Singh, J., Tong, S., Humphrey, C., Clevenger, D., Tan, W., Szekely, B., Wang, Y., Li, Y., Muse, E. A., Kiyono, M., Hanamura, S., Inoue, E., Nakamura, M., Huffman, M. A., Jiang, B. and Nishida, T. (2008). Descriptive epidemiology of fatal respiratory outbreaks and detection of a human-related metapneumovirus in wild chimpanzees (*Pan troglodytes*) at Mahale Mountains National Park, Western Tanzania. *American Journal of Primatology* **70**, 738–744.

Kilbourn, A. M., Karesh, W. B., Wolfe, N. D., Bosi, E. J., Cook, R. A. and Andau, M. (2003). Health evaluation of free-ranging and semi-captive orangutans (*Pongo pygmaeus pygmaeus*) in Sabah, Malaysia. *Journal of Wildlife Diseases* **39**, 73–83.

Knott, C. D. (2001). Female reproductive ecology of the apes: implications for human evolution. In *Reproductive Ecology and Human Evolution* (ed. Ellison, P. T.), pp. 429–463. Walter de Gruyter, New York, USA.

Knott, C. D. (2005). Energetic responses to food availability in the great apes: Implications for hominin evolution. In *Primate Seasonality : Implications for Human Evolution* (ed. Brockman, D. and Van Schaik, C. P.), pp. 351–378. Cambridge University Press, Cambridge, UK.

Landsoud-Soukate, J., Tutin, C. E. G. and Fernandez, M. (1995). Intestinal parasites of sympatric gorillas and chimpanzees in the Lopé Reserve, Gabon. *Annals of Tropical Medicine and Parasitology* **89**, 73–79.

Leeflang, P. D. and Markham, R. J. (1986). Strongyloidosis in orang-utans (*Pongo pygmaeus*) at Perth Zoo: an apparently successful eradication programme. *International Zoo Yearbook* **24**, 256–260. doi: 10.1111/J1748-1090.1985.TB02550-X.

Ley-Vela, M. (2005). Diurnal primate distribution and density in the Sabangau National Park, Central Kalimantan, Indonesia. M.Res. thesis, University of Roehampton, Roehampton, Surrey, UK.

Loehle, C. (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology* **76**, 326–335.

Maggioncalda, A. N., Sapolsky, R. M. and Czekala, N. M. (1999). Reproductive hormone profiles in captive male orangutans: Implications for understanding developmental arrest. *American Journal of Physical Anthropology* **109**, 19–32.

Marti, H. and Escher, E. (1990). SAF – Eine alternative Fixierlösung für parasitologische Stuhluntersuchungen. *Schweizerische Medizinische Wochenschrift* **120**, 1473–1476.

Michaud, C., Tantalean, M., Ique, C., Montoya, E. and Gozalo, A. (2003). A survey for helminth parasites in feral New World non-human primate populations and its comparison with parasitological data from man in the region. *Journal of Medical Primatology* **32**, 341–45.

Miyamoto, M. M., Koop, B. F., Slightom, J. L., Goodman, M. and Tennant, M. R. (1988). Molecular systematics of higher primates: Genealogical relations and classification. *Proceedings of the National Academy of Sciences, USA* **85**, 7627–7631.

Mul, I. F., Paembonan, W., Singleton, I., Wich, S. A. and Van Bolhuis, E. G. (2007). Intestinal parasites of free-ranging, semicaptive, and captive *Pongo abelii* in Sumatra, Indonesia. *International Journal of Primatology* **28**, 407–420. doi: 10.1007/S10764-007-9119-7.

Muller, R. (2002). *Worms and Human Disease*, 2nd edn. CABI Publishing, CABI International, Wallingford, UK.

Norusis, M. J. (1986). *SPSS/PC + Advanced Statistics*, 1st Edn. SPSS Inc., Chicago.

Nunn, C. L. and Altizer, S. (2006). *Infectious Diseases in Primates. Behavior, Ecology and Evolution*, 1st. Edn. Oxford University Press, Oxford, UK.

Ott-Joslin, J. E. (1993). Zoonotic diseases of nonhuman primates. In *Zoo and Wild Animal Medicine: Current Therapy* (ed. Fowler, M. E.), pp. 358–373. W. B. Saunders, Philadelphia, PA, USA.

Packer, C., Altizer, S., Appel, M., Brown, E., Martenson, J., O'Brian, S. J. and Roelke-Parker, M. (1999). Viruses of the Serengeti: patterns of infection and mortality in African lions. *Journal of Animal Ecology* **68**, 1161–1178.

Pusey, A. E., Wilson, M. L. and Collins, D. A. (2008). Human Impacts, Disease Risk, and Population Dynamics in the Chimpanzees of Gombe National Park, Tanzania. *American Journal of Primatology* **70**, 738–744.

Putrali, J., Carney, W. P., Stafford, E. E. and Tubo, S. (1977). Intestinal and blood parasites in the Banggai Kabupaten, Central Sulawesi, Indonesia. *Southeast Southeast Asian Journal of Tropical Medicine and Public Health* **8**, 375–379.

Rijksen, H. D. (1978). *A Field Study on Sumatran Orang Utans* (*Pongo pygmaeus abelli Lesson 1827*): *Ecology, Behaviour and Conservation*. Ph.D. dissertation. Veenan, H. & Zonen B.V., Wageningen, The Netherlands.

Rijksen, H. D. and Meijaard, E. (1999). *Our Vanishing Relative: the Status of Wild Orang-Utans at the Close of the Twentieth Century*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Schmidt, U. (1971). Parasitologische Kotuntersuchung durch ein neues Verduennungsverfahren. *Tieraerztliche Umschau* **26**, 229–230.

Setia, T. M., Delgado, R. A., Utami Atmoko, S. S., Singleton, S. and Van Schaik, C. P. (2009). Social organizsation and male-female relationships. In *Orangutans – Geographic Variation in Behavioral Ecology and Conservation* (ed. Wich, S. A., Utami Atmoko, S. S., Setia, T. M. and Van Schaik, C. P.), pp. 245–253. Oxford University Press, Oxford, UK.

Singleton, I. and Van Schaik, C. P. (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology* **22**, 877–911.

Sleeman, J. M., Meader, L. L., Mudakikwa, A. B., Foster, J. W. and Patton, S. (2000). Gastrointestinal parasites of mountain gorillas (*Gorilla gorilla beringei*) in the Parc National des Volcans, Rwanda. *Journal of Zoo and Wildlife Medicine* **31**, 322–328.

Utami, S. S., Goossens, B., Bruford, M. W., De Ruiter, J. R. and Van Hooff, A. R. A. M. (2002). Male bimaturism and reproductive success in Sumatran orang-utans. *Behavioral Ecology* **13**, 643–652.

Utami Atmoko, S. S., Singleton, I., Van Noordwijk, M. A., Van Schaik, C. P. and Mitra Setia, T. (2009*a*). Male-male relationships in orangutans. In *Orangutans – Geographic Variation in Behavioral Ecology and Conservation* (ed. Wich, S. A., Utami Atmoko, S. S., Setia, T. M. and Van Schaik, C. P.), pp. 225–233. Oxford University Press, Oxford, UK.

Utami Atmoko, S. S., Mitra Setia, T., Goossens, B., James, S. S., Knott, C. D., Morrogh-Bernard, H. C., Van Schaik, C. P. and Van Noordwijk, M. A. (2009*b*). Orangutan mating behaviour and strategies. In *Orangutans – Geographic Variation in Behavioral Ecology and Conservation* (ed. Wich, S. A., Utami Atmoko, S. S., Setia, T. M. and Van Schaik, C. P.), pp. 235–244. Oxford University Press, Oxford, UK.

Van Heuverswyn, F., Li, Y., Neel, C., Bailes, E., Keele, B. F., Liu, W., Loul, S., Butel, C., Liegeois, F., Bienvenue, Y., Ngolle, E. M., Sharp, P. M., Shaw, G. M., Delaporte, E., Hahn, B. H. and Peeters, M. (2006). Human immunodeficiency viruses: SIV infection in wild gorillas. *Nature, London* **444**, 164.

Van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates* **40**, 69–86.

Van Schaik, C. P., Wich, S. A., Utami, S. S. and Odom, K. (2005). A simple alternative to line transects of nests for estimating orangutan densities. *Primates* **46**, 249–254.

Viney, M. E. and Lok, J. B. (2007). *Strongyloides* spp. In *The C. elegans Research Community, WormBook* (ed. Hodgkin, J. and Anderson, P.), www.wormbook.org. doi/10.1895/wormbook.1.141.

Vitone, N. D., Altizer, S. M. and Nunn, C. L. (2004). Body size, diet and sociality influence the species richness of parasitic worms in anthropoid primates. *Evolutionary Ecology Research* **6**, 1–17.

Warren, K. S. (2001). Orangutan conservation – epidemiological aspects of health management and population genetics. Ph.D. dissertation, Murdoch University, Australia.

Wells, S. K., Sargeant, E., Andrews, M. E. and Anderson, D. E. (1990). Gastrointestinal disorders. In *Medical Management of the Orangutan* (ed. Wells, S.), pp. 65–66. The Audobon Institute, Louisiana, USA.

Whitfield, J. (2003). Ape populations decimated by hunting and Ebola virus. *Nature, London* **422**, 551.

Wich, S. A., Meijaard, E., Marshall, A. J., Husson, S., Ancrenaz, M., Lacy, R. C., Van Schaik, C. P., Sugardjito, J., Simorangkir, T., Traylor-Holzer, K., Doughty, M., Supriatna, J., Dennis, R., Gumal, M., Knott, C. D. and Singleton, I. (2008). Distribution and conservation status of the orangutan (*Pongo* spp.) on Borneo and Sumatra: how many remain? *Oryx* **42**, 329–339.

Wich, S. A., Sterck, E. H. M. and Utami, S. S. (1999). Are orangutan females as solitary as chimpanzee females? *Folia Primatologia* **70**, 23–28.

Williams, J. M., Lonsdorf, E. V., Wilson, M. L., Schumacher-Stankey, J., Goodall, J. and Pusey, A. E. (2008). Causes of death in the Kasekela chimpanzees of Gombe National Park, Tanzania. *American Journal of Primatology* **70**, 738–744.

Xu, X. and Arnason, U. (1996). The mitochondrial DNA molecule of Sumatran orangutan and a

molecular proposal for two (Bornean and Sumatran) species of orangutan. *Journal of Molecular Evolution* **43**, 431–437.

Yamagiwa, J. (2004). Diet and foraging of the great apes: ecological constraints on their social organizations and implications for their divergence. In *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence* (ed. Russon, A. E. and Begun, D. R.), pp. 210–233. Cambridge University Press, Cambridge, UK.