Chapter 3
Final Hosts of *Fascioloides magna*

Abstract *Fascioloides magna* parasitizes in a broad spectrum of final hosts, mainly free living and domestic ruminants. Final hosts of giant liver fluke are divided into three types (definitive, dead-end and aberrant) according to interrelationships between the parasite and the host, the ability of fluke to reach maturity and produce eggs, pathological changes within the host organism, and the potential to release eggs of *F. magna* into external environment. Definitive hosts contribute significantly to further spread of propagative stages of *F. magna* into the environment. Mature flukes localized in thin-walled pseudocysts or fibrous capsules in the liver parenchyma can produce eggs and release them into the host's small intestine through the bile system. Definitive hosts tolerate fascioloidosis rather well, and infection is very often subclinical. In dead-end hosts, giant liver fluke can reach the liver but parasite matures very rarely. Only few eggs are produced and they are not released into the bile system. In aberrant hosts, giant liver fluke can not successfully complete the migration; parasite may occasionaly move up to the liver but formation of pseudocysts is not successful. Such hosts may often die due to tissue damage, which is associated with migration of immature flukes through peritoneal, thoracic or abdominal cavities.

Keywords Giant liver fluke · Final host · Definitive host · Dead-end host · Aberrant host · Host-parasite interrelationship · Experimental infection · Natural infection

3.1 Naturally Infected Final Hosts

Natural infections of *F. magna* occur primarily in representatives of the families Cervidae and Bovidae. According to Pybus (2001), there are three basic categories of final hosts: definitive, dead-end and aberrant. Different terminology has been applied throughout the literature in order to designate various types of final hosts of giant liver fluke. In particular "obligate", "specific", "typical" and "normal" have sometimes been used to determine definitive hosts, while terms "non-specific",

I. Králová-Hromadová et al., *The Giant Liver Fluke, Fascioloides magna: Past, Present and Future Research*, SpringerBriefs in Animal Sciences,
DOI 10.1007/978-3-319-29508-4_3

"unspecific", "atypical" and "abnormal" are used to describe dead-end and aberrant hosts. Since the terminology described by Pybus (2001) takes into consideration host-parasite relationships, pathological changes within the final hosts, reproduction and further spread of the parasite, we accept and apply this terminology throughout the publication.

3.1.1 Definitive Hosts

Definitive hosts are characterized by maturation of *F. magna* flukes in thin-walled pseudocysts (fibrous capsules) in the liver parenchyma. Mature flukes produce eggs which are released into the host's small intestine through the bile system. Thus, definitive hosts contribute significantly to further spread of propagative stages (eggs) of *F. magna* into the external environment. All definitive hosts are members of the family Cervidae, and except for the red deer and fallow deer, they are primarily "New World" cervids. From veterinary point of view, infection in this type of hosts is very often subclinical and fascioloidosis is rather well tolerated. The following cervids are considered to be definitive hosts of giant liver fluke:

- white-tailed deer *Odocoileus virginianus*
- wapiti *Cervus elaphus canadensis*
- Rocky Mountain elk *Cervus elaphus nelsoni*
- Roosevelt elk *Cervus elaphus roosevelti*
- caribou *Rangifer tarandus*
- black-tailed deer *Odocoileus hemionus columbianus*
- mule deer *Odocoileus hemionus hemionus*
- red deer *Cervus elaphus elaphus*
- fallow deer *Dama dama*

It is generally known that *F. magna* is of the North American origin where it co-evolved with ancestral *Odocoileus* sp. White-tailed deer has significantly contributed to maintenance and spread of fascioloidosis in North America, and till now it represents one of the most frequent definitive hosts of giant liver fluke. In general, white-tailed deer tolerate *F. magna* infection without significant clinical signs (Pybus 2001).

In North America, *F. magna* was found in naturally infected white-tailed deer coming from all enzootic regions except for NQL (see Table 3.1 and references therein). The most frequent occurrence of fascioloidosis was determined in SAS enzootic region throughout broad spectrum of southeastern US states, with the highest prevalence (64–84 %) in Texas (Foreyt and Todd 1972; Foreyt et al. 1977). White-tailed deer was also attractive "import article", which was introduced to European parks, enclosures and reservations in the 19th and 20th centuries. In Europe, fascioloidosis was detected in white-tailed deer in the Czech Republic (Erhardová-Kotrlá 1971). Besides white-tailed deer, wapiti and caribou have significantly contributed to distribution of *F. magna* within and between enzootic

regions in North America. Both cervids acquired giant liver fluke from white-tailed deer in overlapping regions with sympatric occurrence of different cervids (Kennedy et al. 1999; Bazsalovicsová et al. 2015).

Taxonomy of the genus *Cervus* is not univocal and different authors accept different scientific names and terminology. In general, *Cervus elaphus* is supposed to include many subspecies, including the most frequent "Old World" cervid, red deer *Cervus elaphus elaphus*, and common North American species, wapiti *Cervus elaphus canadensis*. In North America, there are numerous subspecies of *C. elaphus*, including Rocky Mountain elk *Cervus elaphus nelsoni* and Roosevelt elk *Cervus elaphus roosevelti* (Bryant and Maser 1982). Some authors consider red deer and wapiti to be separate species, *Cervus elaphus* and *Cervus canadensis*, respectively (e.g. Groves 2006). In order to avoid any misunderstanding in terminology of deer, we use the original scientific names of all cervids as provided in the reference literature.

Wapiti (Fig. 3.1), one of the largest species of family Cervidae, was found to be infected with *F. magna* mainly in foothills and mountain endemic areas of the Rocky Mountain trench (RMT) enzootic region, in Canadian provinces Montana and Alberta (Banff National Park) (see Table 3.1 and references therein). In NPC enzootic region, fascioloidosis was detected in wapiti from British Columbia and Oregon (Table 3.1). The prevalence detected in RMT and NPC enzootic regions reached up to 80–100 % (Whiting and Tessaro 1994; Hood et al. 1997; Pybus et al. 2015). Sporadic occurrence of *F. magna* in wapiti was detected in Cuba, where it was imported from North America (Lorenzo et al. 1989).

Others "New World" cervids susceptible to *F. magna* infection are Rocky Mountain elk, Roosevelt elk, caribou, black-tailed deer and mule deer (see Table 3.1 and references therein). While Rocky Mountain elk and mule deer were found mainly in RMT region, Roosevelt elk and black-tailed deer infected with *F. magna* were detected in coastal states and provinces of NPC region.

Along with wapiti and white-tailed deer, third dominant definitive host of *F. magna* is reindeer or caribou, terrestrial herbivore of many northern ecosystems (Pollock et al. 2009). The George River herd is the largest caribou population in eastern Canada (mainly Labrador), and represents the only endemic caribou herd in North America infected with *F. magna* (Wobeser et al. 1985; Pollock et al. 2009). Caribou infected with *F. magna* was found only in NQL region, where the dynamics of fascioloidosis is similar to dynamics in populations of wapiti and white-tailed deer (Lankester and Luttich 1988). Excessive number of flukes may lead to mortality even in this type of definitive host (Pybus 2001).

In Europe, the most frequent and dominat definitive host of *F. magna* is red deer. Similarly to white-tailed deer and wapiti in North America, red deer plays an important role in maintaining and spread of fascioloidosis in Europe. Red deer infected with *F. magna* was found in all European natural foci (IT, CZ-PL and DFF) in all countries (see Table 3.1 and references therein). A very high prevalence, reaching up to 100 % was determined in Italy (Balbo et al. 1987), Czech Republic (Erhardová-Kotrlá 1971) and Danube floodplain forests (Rajský et al. 2002; Ursprung and Prosl 2011). Fallow deer is second ruminant species known as

Table 3.1 Spectrum of naturally infected final hosts (DEFINITIVE HOSTS; all family CERVIDAE) with *F. magna*

Definitive host[a]	Natural habitat	Continent	NA region[b] EU focus[c]	US state, CA province[d] EU country[e]	P (%)	References
White-tailed deer *Odocoileus virginianus*	North and South America	North America	NPC	British Columbia	28	Pybus et al. (2015)
		North America	RMT	Alberta	n.i.	Swales (1935)
		North America	RMT	Alberta	2	Pybus (1990)
		North America	RMT	Alberta	44	Pybus et al. (2015)
		North America	RMT	Montana	n.i.	Aiton (1938) c.i. Pybus (2001)
		North America	GLR	Minnesota	n.i.	Fenstermacher et al. (1943)
		North America	GLR	Minnesota	n.i.	Bazsalovicsová et al. (2015)
		North America	GLR	New York	n.i.	Stiles and Hassall (1894) c.i. Pybus (2001)
		North America	SAS	Florida	n.i.	Dinaburg (1939) c.i. Pybus (2001)
		North America	SAS	Florida	n.i.	Bazsalovicsová et al. (2015)
		North America	SAS	Georgia	n.i.	Bazsalovicsová et al. (2015)
		North America	SAS	Kentucky	n.i.	Lydeard et al. (1989)
		North America	SAS	Louisiana	n.i.	Bazsalovicsová et al. (2015)
		North America	SAS	Mississippi	n.i.	Bazsalovicsová et al. (2015)
		North America	SAS	North Carolina	73	Flowers (1996)
		North America	SAS	South Carolina	n.i.	Dinaburg (1939) c.i. Pybus (2001)
		North America	SAS	South Carolina	30	Lydeard et al. (1989)
		North America	SAS	South Carolina	25.6	Lydeard et al. (1989)
		North America	SAS	South Carolina	11.73	Steele (2008)
		North America	SAS	South Carolina	n.i.	Bazsalovicsová et al. (2015)
		North America	SAS	Tennessee	41.9	Lydeard et al. (1989)
		North America	SAS	Tennessee	53.3	Lydeard et al. (1989)
		North America	SAS	Texas	n.i.	Olsen (1949)

(continued)

Table 3.1 (continued)

Definitive host[a]	Natural habitat	Continent	NA region[b] EU focus[c]	US state, CA province[d] EU country[e]	P (%)	References
		North America	SAS	Texas	69.7	Foreyt and Todd (1972)
		North America	SAS	Texas	64–84	Foreyt et al. (1977)
		North America	SAS	13 Southeastern states	12.8	Pursglove et al. (1977)
		Europe	CZ-PL	Czech Republic	n.i.	Erhardová-Kotrlá (1971)
Wapiti *Cervus elaphus canadensis*	North America, Eastern Asia	North America	NPC	Oregon	n.i.	Dutson et al. (1967)
		North America	NPC	British Columbia	n.i.	Flook and Stenton (1969)
		North America	NPC	British Columbia	77–100	Pybus et al. (2015)
		North America	RMT	Alberta	n.i.	Swales (1935)
		North America	RMT	Alberta	n.i.	Flook and Stenton (1969)
		North America	RMT	Alberta	50	Kingscote et al. (1987)
		North America	RMT	Alberta	80	Whiting and Tessaro (1994)
		North America	RMT	Alberta	3.2–33.3	Kennedy et al. (1999)
		North America	RMT	Alberta	53–79	Pybus et al. (2015)
		North America	RMT	Alberta	n.i.	Bazsalovicsová et al. (2015)
		North America	RMT	Montana	n.i.	Butler (1938) c.i. Pybus (2001)
		North America	RMT	Montana	4–100	Hood et al. (1997)
		North America	RMT	Saskatchewan	n.i.	Wobeser et al. (1985)
		Latin America	n.r.	Cuba	n.i.	Lorenzo et al. (1989)
Rocky Mountain elk *Cervus elaphus nelsoni*	Western North America, Rocky Mountains	North America	RMT	Alberta	29	Pybus (1990)
		North America	RMT	Alberta	93	Pybus et al. (1991)
		Europe	IT	Italy	n.i.	Bassi (1875) c.i. Pybus (2001)
Roosevelt elk *Cervus elaphus roosevelti*	Western North America, Alaska	North America	NPC	British Columbia	n.i.	Bazsalovicsová et al. (2015)
		North America	NPC	Washington	n.i.	Schwartz and Mitchell (1945)

(continued)

Table 3.1 (continued)

Definitive host[a]	Natural habitat	Continent	NA region[b] EU focus[c]	US state, CA province[d] EU country[e]	P (%)	References
Caribou, reindeer *Rangifer tarandus*	Northern Europe, North America, Siberia	North America	NQL	Quebec	n.i.	Choquette et al. (1971)
		North America	NQL	Labrador	58	Lankester and Luttich (1988)
		North America	NQL	Labrador	78	Pollock et al. (2009)
		North America	NQL	Labrador	n.i.	Bazsalovicsová et al. (2015)
Black-tailed deer *Odocoileus hemionus columbianus*	Western North America, Alaska	North America	NPC	British Columbia	n.i.	Hadwen (1916) c.i. Pybus (2001)
		North America	NPC	British Columbia	n.i.	Cowan (1946)
		North America	NPC	Oregon	n.i.	Bazsalovicsová et al. (2015)
Mule deer *Odocoileus hemionus hemionus*	Western North America	North America	NPC	British Columbia	4	Pybus et al. (2015)
		North America	RMT	Alberta	14	Pybus (1990)
		North America	RMT	Alberta	6	Pybus et al. (2015)
		North America	RMT	Montana	n.i.	Senger (1963)
Red deer *Cervus elaphus elaphus*	Europe, Western and Central Asia	Europe	IT	Italy	n.i.	Bassi (1875) c.i. Pybus (2001)
		Europe	IT	Italy	51.8	Lanfranchi et al. (1984/85)
		Europe	IT	Italy	50–100	Balbo et al. (1987)
		Europe	IT	Italy	n.i.	Balbo et al. (1989)
		Europe	IT	Italy	n.i.	Králová-Hromadová et al. (2011)
		Europe	CZ-PL	Czech Republic	81–100	Erhardová-Kotrlá (1971)
		Europe	CZ-PL	Czech Republic	n.i.	Kolář (1978)
		Europe	CZ-PL	Czech Republic	4–95	Novobilský et al. (2007)
		Europe	CZ-PL	Czech Republic	n.i.	Králová-Hromadová et al. (2011)
		Europe	CZ-PL	Poland	n.i.	Ślusarski (1955)
		Europe	CZ-PL	Poland	n.i.	Pyziel et al. (2014)
		Europe	CZ-PL	Poland	n.i.	Demiaszkiewicz et al. (2015)
		Europe	CZ-PL	Poland	n.i.	Králová-Hromadová et al. (2015)
		Europe	DFF	Austria	66.7	Winkelmayer and Prosl (2001)

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Table 3.1 (continued)

Definitive host[a]	Natural habitat	Continent	NA region[b] EU focus[c]	US state, CA province[d] EU country[e]	P (%)	References
		Europe	DFF	Austria	15.8	Ursprung et al. (2006)
		Europe	DFF	Austria	13–100	Ursprung and Prosl (2011)
		Europe	DFF	Hungary	≥90	Majoros and Sztojkov (1994)
		Europe	DFF	Hungary	21.1–65.1	Giczi (2008)
		Europe	DFF	Hungary	n.i.	Králová-Hromadová et al. (2011)
		Europe	DFF	Slovakia	70–80	Rajský et al. (1995)
		Europe	DFF	Slovakia	90	Rajský et al. (1996)
		Europe	DFF	Slovakia	70	Špakulová et al. (1997)
		Europe	DFF	Slovakia	91.3	Rajský et al. (2002)
		Europe	DFF	Slovakia	17.39	Rajský et al. (2006)
		Europe	DFF	Slovakia	n.i.	Králová-Hromadová et al. (2011)
		Europe	DFF	Croatia	n.i.	Marinculić et al. (2002)
		Europe	DFF	Croatia	54.1	Janicki et al. (2005)
		Europe	DFF	Croatia	20–80	Slavica et al. (2006)
		Europe	DFF	Croatia	53.3	Rajković-Janje et al. (2008)
		Europe	DFF	Croatia	4.05	Rajković-Janje et al. (2008)
		Europe	DFF	Croatia	0–48	Florijančić et al. (2010)
		Europe	DFF	Croatia	n.i.	Králová-Hromadová et al. (2011)
		Europe	DFF	Croatia	57.4	Severin et al. (2012)
		Europe	n.d.	Germany	n.i.	Salomon (1932)
		Europe	n.d.	Germany	70	Rehbein et al. (2012)
		Europe	n.d.	Germany	4.9	Plötz et al. (2015)

(continued)

Table 3.1 (continued)

Definitive host[a]	Natural habitat	Continent	NA region[b] EU focus[c]	US state, CA province[d] EU country[e]	P (%)	References
Fallow deer *Dama dama*	Western Eurasia	Europe	IT	Italy	n.i	Bassi (1875) c.i. Pybus (2001)
		Europe	CZ-PL	Czech Republic	n.i.	Ullrich (1930)
		Europe	CZ-PL	Czech Republic	21.6–31.9	Erhardová-Kotrlá (1971)
		Europe	CZ-PL	Czech Republic	15.8	Chroust and Chroustová (2004)
		Europe	CZ-PL	Czech Republic	4–95	Novobilský et al. (2007)
		Europe	CZ-PL	Poland	n.i.	Demiaszkiewicz et al. (2015)
		Europe	n.d.	Poland	n.i.	Karamon et al. (2015)
		Europe	DFF	Austria	n.i.	Pfeiffer (1983)
		Europe	DFF	Serbia	52.2	Marinković et al. (2013)
		Europe	n.d.	Germany	10.2	Plötz et al. (2015)

NA North America, *CA* Canada, *EU* Europe, *P (%)* prevalence of *Fascioloides magna* infection, *NPC* northern Pacific coast, *RMT* Rocky Mountain trench, *GLR* Great Lakes region, *NQL* northern Quebec and Labrador, *SAS* Gulf coast, lower Mississippi and southern Atlantic seaboard, *IT* Italy, *CZ-PL* Czech Republic and southwestern Poland, *DFF* Danube floodplain forests, *FM Fascioloides magna*, *n.i.* not indicated in the respective literature, *n.r.* not relevant, *n.d.* not detected, *c.i.* cited in

[a]Order of definitive hosts follows the one indicated by Pybus (2001)

[b]North American enzootic regions are listed in west-east and north-south directions

[c]European natural foci are listed chronologically, according to first discoveries in the respective focus

[d]US states and Canadian provinces are listed alphabetically within the respective enzootic region

[e]European countries are listed chronologically, according to first discoveries in the respective country

Fig. 3.1 Wapiti (*Cervus elaphus canadensis*) from Banff National Park, Alberta, Canada. (*Photo* I. Králová-Hromadová)

definitive host of *F. magna* in Europe; fascioloidosis in fallow deer was detected in all natural foci (Table 3.1); the highest prevalence was reported from Czech Republic reaching up to 95 % (Novobilský et al. 2007).

The prevalence of fascioloidosis in definitive hosts is age-dependent. While young hosts are rarely infected, infection is increasing in older age classes (Flook and Stenton 1969; Foreyt et al. 1977; Lankester and Luttich 1988; Mulvey and Aho 1993). Prevalence of adult flukes is comparable in both sexes in wapiti (Pybus 2001), white-tailed deer (Foreyt et al. 1977), and caribou (Lankester and Luttich 1988).

3.1.2 Dead-End Hosts

In dead-end hosts, giant liver fluke can reach the liver but the parasite matures very rarely and few produced eggs are usually not released into the bile system, intestine and further to the external environment. Contrary to definitive hosts, dead-end hosts do not contribute to maintenance of the infection and spread of propagative stages of *F. magna.* Fascioloidosis in this type of hosts may have a lethal effect. Dead-end hosts represent taxonomically diverse category, in particular:

Family Cervidae

- moose *Alces alces*
- sika deer *Cervus nippon*
- sambar deer *Cervus unicolor*

Family Bovidae

- cattle *Bos taurus*
- bison *Bison bison*
- yak *Bos grunniens*
- blue bull *Boselaphus tragocamelus*
- muscox *Ovibus moschatus*

Family Equidae

- horse *Equus* sp.

Family Suidae

- wild boar *Sus scrofa*
- domestic swine *Sus scrofa* f. *domestica*

Family Tayassuidae

- collared peccary *Pecari tajacu*

Family Camelidae

- llama *Lama glama*

Moose represents one of the most frequent dead-end hosts of the family Cervidae. Fascioloidosis in this type of host was detected in NPC, RMT and GLR enzootic regions (see Table 3.2 and references therein), with the highest prevalence determined in British Columbia (63 %; Pybus et al. 2015) and Minnesota (89 %; Murray et al. 2006). In Europe, sika deer was found to be infected with *F. magna* in Czech Republic and Germany (Erhardová-Kotrlá 1971; Rehbein et al. 2012; Plötz et al. 2015).

Regarding domestic ruminants, a cattle represents the most common dead-end host of *F. magna* in North America and Europe. Giant liver fluke mature in the liver, eggs are produced, but stay trapped within hepatic parenchyma and do not enter bile ducts (Foreyt and Todd 1976). Fascioloidosis in cattle causes chronic liver lesions (Price 1953), but the infection is usually not lethal (Lankester 1974; Foreyt and Todd 1976; Foreyt and Parish 1990). Cattle infected with *F. magna* was reported in all North American enzootic regions except for NQL, and in two European countries, Italy and Czech Republic (see Table 3.2 and references therein). A sporadic occurrence was detected in South Africa (Boomker and Dale-Kuys 1977) and Australia (Arundel and Hamir 1982). Within the family Bovidae, *F. magna* infections were also found in bison and yak from Alberta (RMT) (Cameron 1923 c.i. Pybus 2001; Swales 1935), in muskox from Quebec (NQL) (Bazsalovicsová et al. 2015), and in blue bull from Italy (Bassi 1875 c.i. Pybus 2001).

A rather rare dead-end host of *F. magna* is wild boar; infections were documented in Italy (Balbo et al. 1987, 1989) and Texas, with high prevalence ranging from 51.7 % (Foreyt and Todd 1972) to 69 % (Foreyt et al. 1975). Dangerous for pigs may be feeding on pastures contaminated by eggs of infected white-tailed deer, or other definitive hosts (Schwartz et al. 1993). Wild boar does not shed *F. magna*

Table 3.2 Spectrum of naturally infected final hosts (DEAD-END HOSTS) with *F. magna*

Dead-end host[a]	Family	Natural habitat	Continent	NA region[b] EU focus[c]	US state CA province[d] EU country[e]	P (%)	References
Moose *Alces alces*	Cervidae	Canada, Alaska, Scandinavia, Rusia	North America	NPC	British Columbia	n.i.	Hilton (1930) c.i. Pybus (2001)
			North America	NPC	British Columbia	n.i.	Cowan (1951)
			North America	NPC	British Columbia	63	Pybus et al. (2015)
			North America	RMT	Alberta	4	Pybus (1990)
			North America	RMT	Alberta	52	Pybus et al. (2015)
			North America	RMT	Saskatchewan	n.i.	Wobeser et al. (1985)
			North America	GLR	Manitoba	n.i.	Lankester (1974)
			North America	GLR	Minnesota	n.i.	Fenstermacher (1934) c.i. Pybus (2001)
			North America	GLR	Minnesota	89	Murray et al. (2006)
			North America	GLR	Minnesota	17.4; 5.2	Peterson et al. (2013)
			North America	GLR	North Dakota	0–19.6	Maskey (2011)
			North America	GLR	Ontario	n.i.	Kingscote (1950)
Sika deer *Cervus nippon*	Cervidae	Eastern Asia	Europe	CZ-PL	Czech Republic	4	Erhardová-Kotrlá (1971)
			Europe	n.d.	Germany	37.5	Rehbein et al. (2012)
			Europe	n.d.	Germany	0	Plötz et al. (2015)
Sambar deer *Cervus unicolor*	Cervidae	Southern and Southeastern Asia	Europe	IT	Italy	n.i.	Bassi (1875) c.i. Pybus (2001)

(continued)

Table 3.2 (continued)

Dead-end host[a]	Family	Natural habitat	Continent	NA region[b] EU focus[c]	US state CA province[d] EU country[e]	P (%)	References
Cattle *Bos taurus*	Bovidae	Worldwide distribution, domesticated	North America	NPC	British Columbia	n.i.	Hilton (1930) c.i. Pybus (2001)
			North America	RMT	Alberta	n.i.	Swales (1935)
			North America	RMT	Montana	17.24	Knapp et al. (1992)
			North America	RMT	Saskatchewan	n.i.	Wobeser and Schumann (2014)
			North America	GLR	Michigan	0.41–13.9	Schillhorn van Veen (1987)
			North America	SAS	Texas	n.i.	Francis (1891) c.i. Pybus (2001)
			North America	SAS	Texas	38.3	Foreyt and Todd (1972)
			Europe	IT	Italy	3.4	Lanfranchi et al. (1984/85)
			Europe	IT	Italy	3.7	Balbo et al. (1987)
			Europe	CZ-PL	Czech Republic	n.i.	Záhoř et al. (1966)
			Europe	CZ-PL	Czech Republic	9.1–21.1	Chroustová et al. (1980)
			Europe	CZ-PL	Czech Republic	n.i.	Leontovyč et al. (2014)
			South Africa	n.r.	n.i.	n.i.	Boomker and Dale-Kuys (1977)
			Australia	n.r.	n.i.	n.i.	Arundel and Hamir (1982)
Bison *Bison bison*	Bovidae	Western Europe, Central Asia, North America	North America	RMT	Alberta	n.i.	Cameron (1923) c.i. Pybus (2001)
			North America	RMT	Alberta	n.i.	Swales (1935)
Yak *Bos grunniens*	Bovidae	Southern Asia	North America	RMT	Alberta	n.i.	Swales (1935)
Blue bull *Boselaphus tragocamelus*	Bovidae	Southern Asia	Europe	IT	Italy	n.i.	Bassi (1875) c.i. Pybus (2001)

(continued)

Table 3.2 (continued)

Dead-end host[a]	Family	Natural habitat	Continent	NA region[b] EU focus[c]	US state CA province[d] EU country[e]	P (%)	References
Muskox *Ovibus moschatus*	Bovidae	Canadian Arctic, Greenland	North America	NQL	Quebec	n.i.	Bazsalovicsová et al. (2015)
Horse *Equus* sp.	Equidae	Worldwide distribution, domesticated	North America	GLR	Minnesota	n.i.	McClanahan et al. (2005)
			Europe	IT	Italy	5.7	Balbo et al. (1987)
Wild boar *Sus scrofa*	Suidae	Eurasia, North Africa, Greater Sunda Islands, USA	North America	SAS	Texas	51.7	Foreyt and Todd (1972)
			North America	SAS	Texas	69	Foreyt et al. (1975)
			North America	SAS	Texas	n.i.	Schwartz et al. (1993)
			Europe	IT	Italy	n.i.	Balbo et al. (1987)
			Europe	IT	Italy	n.i.	Balbo et al. (1989)
Collared peccary *Pecari tajacu*	Tayassuidae	North, Central, South America	North America	SAS	Texas	1	Samuel and Low (1970)
Llama *Lama glama*	Camelidae	South America, domesticated	North America	GLR	Minnesota	n.i.	Conboy et al. (1988)

NA North America, *CA* Canada, *EU* Europe, *P (%)* prevalence of *Fascioloides magna* infection, *NPC* northern Pacific coast, *RMT* Rocky Mountain trench, *GLR* Great Lakes region, *NQL* northern Quebec and Labrador, *SAS* Gulf coast, lower Mississippi and southern Atlantic seaboard, *IT* Italy, *CZ-PL* Czech Republic and southwestern Poland, *DFF* Danube floodplain forests, *n.i.* not indicated in the respective literature, *n.r.* not relevant, *n.d.* not detected, *c.i.* cited in

[a]Order of dead-end hosts follows the one indicated by Pybus (2001)

[b]North American enzootic regions are listed in west-east and north-south directions

[c]European natural foci are listed chronologically, according to first discoveries in the respective focus

[d]US states and Canadian provinces are listed alphabetically within the respective enzootic region

[e]European countries are listed chronologically, according to first discoveries in the respective country

eggs to environment and, therefore, does not contribute to further spread of fascioloidosis (Foreyt et al. 1975). Rare *F. magna* infections were detected in horse (McClanahan et al. 2005) and llama (Conboy et al. 1988) from Minnesota (GLR), in horse from Italy (Balbo et al. 1987), and in collared peccary from Texas (SAS) (Samuel and Low 1970).

3.1.3 Aberrant Hosts

In aberrant hosts, giant liver fluke can not successfully complete migration within the ruminant host; parasite may move up to the liver but formation of pseudocysts is not successful. These hosts may often die due to tissue damage, which is associated with migration of immature flukes through peritoneal, thoracic or abdominal cavities. According to Pybus (2001), aberrant hosts are mainly domestic, but also free living ruminants:

Family Bovidae

- domestic sheep *Ovis aries*
- domestic goat *Capra hircus*
- chamois *Rupicapra rupicapra*
- bighorn sheep *Ovis canadensis*
- mouflon *Ovis orientalis*

Family Cervidae

- roe deer *Capreolus capreolus*

In aberrant hosts, such as sheep and goat, unrestricted migration of fluke through the liver, lungs and peritoneal cavities is typical. It results to massive tissue damage, usually with fatal effects caused even by relatively low intensity of infection (Conboy and Stromberg 1991). Fascioloidosis in domestic sheep and goat was documented both in North America and Europe (see Table 3.3 and references therein). Roe deer, the only cervid species recognized as an aberrant host, was found to be infected with *F. magna* only in Europe, in particular CZ-PL and DFF (see Table 3.3 and references therein). The highest prevalence of fascioloidosis in roe deer was detected in Czech Republic (70–80 %; Erhardová-Kotrlá 1971) and Slovakia (60 %; Rajský et al. 2002).

3.2 Experimentally Infected Final Hosts

The experimental infections of different types of final hosts with *F. magna* were aimed to determine the clinical signs, pathological changes and immunological responses of final hosts under controlled experimental conditions. The major

Table 3.3 Spectrum of naturally infected final hosts (ABERRANT HOSTS) with *F. magna*

Aberrant host[a]	Family	Natural habitat	Continent	NA region[b] EU focus[c]	US state, CA province[d] EU country[e]	P (%)	References
Domestic sheep *Ovis aries*	Bovidae	Worldwide distribution, domesticated	North America	NPC	Oregon	34.3	Foreyt and Hunter (1980)
			North America	RMT	Montana	n.i.	Hall (1914) c.i. Pybus (2001)
			North America	GLR	Wisconsin	n.i.	Campbell and Todd (1954)
			North America	SAS	Texas	n.i.	Olsen (1949)
			Europe	IT	Italy	n.i.	Bassi (1875) c.i. Pybus (2001)
Domestic goat *Capra hircus*	Bovidae	Worldwide distribution, domesticated	North America	SAS	Texas	n.i.	Olsen (1949)
			Europe	IT	Italy	n.i.	Bassi (1875) c.i. Pybus (2001)
Roe deer *Capreolus capreolus*	Cervidae	Eurasia	Europe	CZ-PL	Czech Republic	n.i.	Záhoř (1965)
			Europe	CZ-PL	Czech Republic	70–80	Erhardová-Kotrlá (1971)
			Europe	CZ-PL	Czech Republic	9.1	Chroust and Chroustová (2004)
			Europe	CZ-PL	Poland	n.i.	Demiaszkiewicz et al. (2015)
			Europe	DFF	Austria	n.i.	Winkelmayer and Prosl (2001)
			Europe	DFF	Austria	n.i.	Ursprung et al. (2006)
			Europe	DFF	Hungary	3.7	Giczi (2008)
			Europe	DFF	Slovakia	60	Rajský et al. (2002)
			Europe	DFF	Slovakia	n.i.	Rajský et al. (2006)
			Europe	n.d.	Germany	20	Rehbein et al. (2012)

NA North America, *CA* Canada, *EU* Europe, *P (%)* prevalence of *Fascioloides magna* infection, *NPC* northern Pacific coast, *RMT* Rocky Mountain trench, *GLR* Great Lakes region, *NQL* northern Quebec and Labrador, *SAS* Gulf coast, lower Mississippi and southern Atlantic seaboard, *IT* Italy, *CZ-PL* Czech Republic and southwestern Poland, *DFF* Danube floodplain forests, *n.i.* not indicated in the respective literature, *n.d.* not detected, *c.i.* cited in

[a]Order of aberrant hosts follows the one indicated by Pybus (2001)

[b]North American enzootic regions are listed in west-east and north-south directions

[c]European natural foci are listed chronologically, according to first discoveries in the respective focus

[d]US states and Canadian provinces are listed alphabetically within the respective enzootic region

[e]European countries are listed chronologically, according to first discoveries in the respective country

Table 3.4 Results on experimental infections of different types of final hosts infected with *F. magna*

Experimental animal	No. of meta	Primary localization	Localization in other organs	FM eggs in faeces	Conclusions of experiments	References
White-tailed deer (DH)	500	Liver	Lungs	n.i.	Early prepatent FM infection revealed mild transitory anemia and extensive migration of immature flukes	Presidente et al. (1980)
	50–500	Liver	n.i.	Yes	No significant clinical signs	Foreyt and Todd (1979)
	40–500	Liver	n.i.	Yes	Confirmed definitive host	Foreyt and Todd (1976)
	100	n.i.	n.i.	Yes	Infected animal remained clinically healthy	Foreyt (1996a)
	500	Liver	Lungs Abdominal cavity Thoracic cavity	Yes	No significant clinical signs	Foreyt (1992)
Wapiti (DH)	2,000	Liver	Peritoneal cavity	n.i.	Lethal effect	Foreyt (1996a)
	250	Liver	n.i.	Yes	No significant clinical signs	Foreyt (1996a)
Mule deer (DH)	500	Liver	Lungs Pleural cavity Peritoneal cavity	No	Poor appetite, depression, weakness, lethal effect	Foreyt (1992)
	50	Liver	n.i.	Yes	Confirmed definitive host	Foreyt (1996b)
	250	Liver	n.i.	Yes	Depression, droopy ears, weakness, lethal effect	Foreyt (1996b)

(continued)

Table 3.4 (continued)

Experimental animal	No. of meta	Primary localization	Localization in other organs	FM eggs in faeces	Conclusions of experiments	References
Fallow deer (DH)	32–120	Liver	Peritoneal cavity Abdominal cavity	Yes	Poor appetite, apathy, paroxysm, lethal effect	Erhardová-Kotrlá and Blažek (1970)
Moose (DEH)	50–225	Liver	n.i.	n.i.	Depressed appetite 10 days after infection, later no significant clinical signs	Lankester and Foreyt (2011)
Cattle (DEH)	60	Liver	n.i.	No	No significant clinical signs, later meteorism, poor appetite	Erhardová-Kotrlá and Blažek (1970)
	10–500	Liver	Lungs	No	Eggs retained in the liver	Foreyt and Todd (1976)
	1,000	Liver	Abdominal cavity	n.i.	Well tolerated infection, no clinical signs observed	Conboy and Stromberg (1991)
Bison (DEH)	600	None	n.i.	No	Not developed FM infection	Foreyt and Drew (2010)
Llama (DEH)	250	Liver	n.i.	No	Clinical signs similar to those detected in cattle	Foreyt and Parish (1990)
Sheep (AH)	8–200	Liver	Lungs Abdominal cavity	No	Lethal effect	Foreyt and Todd (1976)
Bighorn sheep (AH)	50	Liver	n.i.	No	Lethal effect	Erhardová-Kotrlá and Blažek (1970)
	50–100	Liver	Lungs Peritoneal cavity	n.i.	Lethal effect	Foreyt (1996a)

(continued)

Table 3.4 (continued)

Experimental animal	No. of meta	Primary localization	Localization in other organs	FM eggs in faeces	Conclusions of experiments	References
Chamois (AH)	250–320	Liver	Lungs	No	No significant clinical signs, lethal effect	Erhardová-Kotrlá and Blažek (1970)
Guinea pig (AH)	20	Liver	Lungs Abdominal cavity Thoracic cavity Sceletal muscle Subcutaneous tissue	n.i.	Lethal effect Infection similar to FM infection in sheep Guinea pigs—possible models for FM infection studies in sheep	Conboy and Stromberg (1991)
	10	Liver	Peritoneal cavity	n.i.	Lethal effect	Foreyt and Todd (1979)

DH definitive host, *DEH* dead-end host, *AH* aberrant host, *No. of meta* number of metacercariae used for infection, *FM Fascioloides magna*, n.i. not indicated

contribution in this field has to be addressed to William J. Foreyt from Washington State University in Pullman, Washington, USA.

Experimental infections were studied in all types of final hosts of *F. magna*, in particular in definitive hosts (white-tailed deer, wapiti, mule deer and fallow deer), dead-end hosts (moose, cattle, bison and llama), and aberrant hosts (sheep, bighorn sheep, chamois and guinea pig) (see Table 3.4 and references therein). The animals were infected with dose of 8–2,000 infective stages (metacercariae) per animal, most frequently in the number of 200–500. The main monitored parameters were localization of parasite, ability of parasite to reach the maturity, detection of *F. magna* eggs in host's faeces and determination of overall clinical signs of infected hosts (including lethal effect). In some cases, haematological and blood chemistry values were determined, as well. The results on experimental infections can be correlated with data known from natural infections; the classification of final hosts can thus be determined in more details.

The majority of experiments were performed in white-tailed deer, the primary definitive host of *F. magna*. The fluke was localized in liver, with occasional occurence in lungs, abdominal and thoracic cavities (see Table 3.4 and references therein). The important finding was detection of *F. magna* eggs in feaces of white-tailed deer, what clearly demonstrates its ability to provide suitable conditions for parasite's maturity, production of eggs, their release into the external environment and consequent spread of the infection.

White-tailed deers were without significant clinical signs and were confirmed to be definitive host for *F. magna*. Presidente et al. (1980) studied haematological values of white-tails infected experimentally with *F. magna*. A reduction of erythrocytes and an elevation of reticulocytes, macrocytic cells and eosinophils were detected in the mentioned study. On the other hand, serum proteins, albumins and globulins remained under the physiological values. Another study confirmed decrease of haemoglobin, increase of total serum proteins, β- and γ-globulin fractions (Foreyt and Todd 1979).

In wapiti, localization of parasite in liver and peritoneal cavity was detected (Foreyt 1996a). Using 250 metacercariae as an infectious dose, no significant clinical signs were recorded and eggs of *F. magna* were detected in faeces. However, a massive infection of wapiti (2,000 metacercariae as infectious dose) was proved to have a lethal effect (Foreyt 1996a). Lethal effect was determined also after experimental infection of mule deer (Foreyt 1992, 1996b), in which giant liver fluke was primarily localized in liver, but even in lungs, pleural and peritoneal cavities; eggs of *F. magna* were found in faecal samples of mule deer. At the end of experimental infection of fallow deer, poor appetite, apathy and paroxysm appeared, and increased γ-globulins and hypoalbuminaemia were detected. Infection had a lethal effect; flukes were found in the liver, peritoneal and abdominal cavities (Erhardová-Kotrlá and Blažek 1970).

In dead-end hosts (moose, cattle and llama) experimentally infected with *F. magna*, dominant localization of the parasite was liver (Erhardová-Kotrlá and Blažek 1970; Foreyt and Todd 1976; Foreyt and Parish 1990; Conboy and Stromberg 1991; Lankester and Foreyt 2011), although presence of *F. magna* was

confirmed also in lungs and abdominal cavity of cattle (Foreyt and Todd 1976; Conboy and Stromberg 1991). The important finding in all studied dead-end hosts was that eggs were not released into faeces, but were found to be retained in liver (Foreyt and Todd 1976). These results correspond to definition of dead-end hosts, which do not contribute to spread of propagative stages of the parasite into external environment. No clinical signs were detected in moose (Lankester and Foreyt 2011) and cattle (Conboy and Stromberg 1991). Fascioloidosis did not develop in experimentally infected bison (Foreyt and Drew 2010).

Experimental infections in aberrant hosts (sheep and bighorn sheep) revealed presence of parasite in liver, but also in lungs, peritoneal and abdominal cavities; fascioloidosis in this type of hosts had a lethal effect (Erhardová-Kotrlá and Blažek 1970; Foreyt and Todd 1976; Foreyt 1996a). In chamois experimentally infected with *F. magna*, no clinical signs were observed during the whole period of experiment. However, on the 138th day after infestation the chamois suddenly died and flukes were found in liver and lungs (Erhardová-Kotrlá and Blažek 1970). As generally known for aberrant hosts, eggs were not detected in faeces.

Already small dose of infective metacercariae (10 and 20) resulted in lethal effect of fascioloidosis in guinea pig, in which natural infections were not determined. As expected, the infection was quite extensive; except for liver, flukes were determined in lungs, peritoneal, abdominal and thoracic cavities, and even in skeletal muscles and subcutaneous tissues (Foreyt and Todd 1979; Conboy and Stromberg 1991). The response observed in guinea pigs was similar to that reported in sheep, suggesting the suitability of the guinea pig as a model for *F. magna* infection in sheep (Conboy and Stromberg 1991).

References

Aiton JF (1938) Enlarged spleen in white-tailed deer at Glacier National Park. Transactions of the North American Wildlife Conference 3:890–892. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Arundel JH, Hamir AN (1982) *Fascioloides magna* in cattle. Aust Vet J 58:35–36

Balbo T, Lanfranchi P, Rossi L, Meneguz PG (1987) Health management of a red deer population infected by *Fascioloides magna* (Bassi, 1875) Ward, 1917. Ann Fac Med Vet Torino 32:1–13

Balbo T, Rossi P, Meneguz PG (1989) Integrated control of *Fascioloides magna* infection in Northern Italy. Parassitologia 31:137–144

Bassi R (1875) Sulla cachessia ittero-verminosa, o marciaia, causta dei Cervi, causata dal *Distomum magnum*. Il Medico Veterinario 4:497–515. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Bazsalovicsová E, Králová-Hromadová I, Štefka J, Minárik G, Bokorová S, Pybus M (2015) Genetic interrelationships of North American populations of giant liver fluke *Fascioloides magna*. Parasit Vectors 8:1–15. doi:10.1186/s13071-015-0895-1

Boomker J, Dale-Kuys JC (1977) First report of *Fascioloides magna* (Bassi, 1875) in South Africa. Onderstepoort J Vet Res 44:49–52

Bryan LD, Maser C (1982) Classification and distribution. In: Thomas JW, Toweill DE, Metz DP (eds) Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania

Butler WJ (1938) Wild animal disease investigation. Montana Livestock Sanitary Board 1:18–19. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Cameron AE (1923) Notes on buffalo: Anatomy, pathological conditions, and parasites. Brit Vet J 79:331–336. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Campbell WC, Todd AC (1954) Natural infections of *Fascioloides magna* in Wisconsin sheep. J Parasitol 40:100

Choquette LPE, Gibson GG, Simard B (1971) *Fascioloides magna* (Bassi, 1875) Ward, 1917 (Trematoda) in woodland caribou, *Rangifer tarandus caribou* (Gmelin), of northeastern Quebec, and its distribution in wild ungulates in Canada. Can J Zool 49:280–281

Chroust K, Chroustová E (2004) Motolice obrovská (*Fascioloides magna*) u spárkaté zvěře v jihočeských lokalitách. Veterinářství 54:296–304 (in Czech)

Chroustová E, Hůlka J, Jaroš J (1980) Prevence a terapie fascioloidózy skotu bithionolsulfoxidem. Vet Med (Praha) 25:557–563 (in Czech)

Conboy GA, Stromberg BE (1991) Hematology and clinical pathology of experimental *Fascioloides magna* infection in cattle and guinea pigs. Vet Parasitol 40:241–255

Conboy GA, O'Brien TD, Stevens DL (1988) A natural infection of *Fascioloides magna* in a llama (*Lama glama*). J Parasitol 74:345–346

Cowan IM (1946) Parasites, diseases, injuries, and anomalies of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), in British Columbia. Can J Res 24:71–103

Cowan IM (1951) The diseases and parasites of big game mammals of western Canada. Proc Ann Game Convention 5:37–64

Demiaszkiewicz AW, Kuligowska I, Pyziel AM, Lachowicz J, Kowalczyk R (2015) Extension of occurrence area of the American fluke *Fascioloides magna* in south-western Poland. Ann Parasitol 61:93–96

Dinaburg AG (1939) Helminth parasites collected from deer, *Odocoileus virginianus* in Florida. Proc Helminthol Soc Wash 6:102–104. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Dutson VJ, Shaw JN, Knapp SE (1967) Epizootiologic factors of *Fascioloides magna* (Trematoda) in Oregon and southern Washington. Am J Vet Res 28:853–860

Erhardová-Kotrlá B (1971) The occurrence of *Fascioloides magna* (Bassi, 1875) in Czechoslovakia. Czechoslovak Academy of Sciences, Prague

Erhardová-Kotrlá B, Blažek K (1970) Artificial infestation caused by the fluke *Fascioloides magna*. Acta Vet Brno 39:287–295

Fenstermacher R (1934) Diseases affecting moose. Alumni Q 22:81–94. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Fenstermacher R, Olsen WO, Pomeroy BS (1943) Some diseases of white-tailed deer in Minnesota. Cornell Vet 33:323–332

Flook DR, Stenton JE (1969) Incidence and abundance of certain parasites in wapiti in the national parks of the Canadian Rockies. Can J Zool 47:795–803. doi:10.1139/z69-138

Florijančić T, Ozimec S, Opačak A, Bošković I, Jelkić D, Marinculić A, Janicki Z (2010) Importance of the Danube River in spreading the infection of red deer with *Fascioloides magna* in eastern Croatia. Paper presented at 38th IAD Conference, Dresden, Germany, 22–25 June 2010

Flowers J (1996) Notes on the life history of *Fascioloides magna* (Trematoda) in North Carolina. J Elisha Mitch Sci S 112:115–118

Foreyt WJ (1992) Experimental *Fascioloides magna* infections of mule deer (*Odocoileus hemionus hemionus*). J Wildl Dis 28:183–187. doi:10.7589/0090-3558-28.2.183

Foreyt WJ (1996a) Susceptibility of bighorn sheep (*Ovis canadensis*) to experimentally-induced *Fascioloides magna* infections. J Wildlife Dis 32:556–559
Foreyt WJ (1996b) Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) as experimental definitive hosts for *Fascioloides magna*. J Wildlife Dis 32:603–606
Foreyt WJ, Todd AC (1972) The occurrence of *Fascioloides magna* and *Fasciola hepatica* together in the livers of naturally infected cattle in South Texas, and the incidence of the flukes in cattle, white-tailed deer, and feral hogs. J Parasitol 58:1010–1011
Foreyt WJ, Todd AC (1976) Liver flukes in cattle: prevalence, distribution and experimental treatment. Vet Med Small Anim Clin 71:816–822
Foreyt WJ, Todd AC (1979) Selected clinicopathologic changes associated with experimentally induced *Fascioloides magna* infection in white-tailed deer. J Wildl Dis 15:83–89
Foreyt WJ, Hunter RL (1980) Clinical *Fascioloides magna* infection in sheep in Oregon on pasture shared by Columbian white-tailed deer. Am J Vet Res 41:1531–1532
Foreyt WJ, Parish S (1990) Experimental infection of liver flukes (*Fascioloides magna*) in a llama (*Lama glama*). J Zoo Wildl Med 21:468–470
Foreyt WJ, Drew ML (2010) Experimental infection of liver flukes, *Fasciola hepatica* and *Fascioloides magna*, in bison (*Bison bison*). J Wildlife Dis 46:283–286. doi:10.7589/0090-3558-46.1.283
Foreyt WJ, Todd AC, Foreyt K (1975) *Fascioloides magna* (Bassi, 1875) in feral swine from southern Texas. J Wildlife Dis 11:554–559. doi:10.7589/0090-3558-11.4.554
Foreyt WJ, Samuel WM, Todd AC (1977) *Fascioloides magna* in white-tailed deer (*Odocoileus virginianus*): observation of the pairing tendency. J Parasitol 63:1050–1052. doi:10.2307/3279843
Francis M (1891) Liver flukes. Tex AES Bull 18:123–136. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames
Giczi E (2008) *Fascioloides magna* (Bassi, 1875) infection of Hungarian red deer and roe deer stock and the possibility of protection. Dissertation, University of West Hungary
Groves C (2006) The genus *Cervus* in eastern Eurasia. Eur J Wildl Res 52:14–22. doi:10.1007/s10344-005-0011-5
Hadwen S (1916) A new host for *Fasciola magna*, Bassi, together with observation on the distribution of *Fasciola hepatica*, L. in Canada. J Am Vet Med Assoc 49:511–515. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames
Hall MC (1914) Society proceedings of the Helminthological Society of Washington. J Parasitol 1:106. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames
Hilton G (1930) Report of the Veterinary Director General, Department of Agriculture, Ottawa, Canada. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames
Hood BR, Rognlie MC, Knapp SE (1997) Fascioloidiasis in game-ranched elk from Montana. J Wildl Dis 33:882–885. doi:10.7589/0090-3558-33.4.882
Janicki Z, Konjević D, Severin K (2005) Monitoring and treatment of *Fascioloides magna* in semi-farm red deer husbandry in Croatia. Vet Res Commun 29:83–88. doi:10.1007/s11259-005-0027-z
Karamon J, Larska M, Jasik A, Sell B (2015) First report of the giant liver fluke (*Fascioloides magna*) infection in farmed fallow deer (*Dama dama*) in Poland—pathomorphological changes and molecular identification. Bull Vet Inst Pulawy 59:339–344. doi:10.1515/bvip-2015-0050
Kennedy MJ, Acorn RC, Moraiko DT (1999) Survey of *Fascioloides magna* in farmed wapiti in Alberta. Can Vet J 40:252–254
Kingscote AA (1950) Liver rot (Fascioloidiasis) in ruminants. Can J Comp Med Vet Sci 14:203–208
Kingscote BF, Yates WDG, Tiffin GB (1987) Diseases of wapiti utilizing cattle range in southwestern Alberta. J Wildl Dis 23:86–91

Knapp SE, Dunkel AM, Han K, Zimmerman LA (1992) Epizootiology of fascioliasis in Montana. Vet Parasitol 42:241–246

Kolář Z (1978) Příspěvek k léčbě fascioloidózy u jelení zvěře. Veterinářství 28:276–277 (in Czech)

Králová-Hromadová I, Bazsalovicsová E, Štefka J, Špakulová M, Vávrová S, Szemes T, Tkach V, Trudgett A, Pybus M (2011) Multiple origins of European populations of the giant liver fluke *Fascioloides magna* (Trematoda: Fasciolidae), a liver parasite of ruminants. Int J Parasitol 41:373–383. doi:10.1016/j.ijpara.2010.10.010

Králová-Hromadová I, Bazsalovicsová E, Demiaszkiewicz A (2015) Molecular characterization of *Fascioloides magna* (Trematoda: Fascioloidae) from south-western Poland based on mitochondrial markers. Acta Parasitol 60:544–547. doi:10.1515/ap-2015-0077

Lanfranchi P, Tolari F, Forletta R, Meneguz PG, Rossi L (1984/85) The red deer as reservoir of parasitic and infectious pathogens for cattle. Ann Fac Med Vet Torino 30:1–17

Lankester MW (1974) *Parelaphostrongylus tenuis* (Nematoda) and *Fascioloides magna* (Trematoda) in moose of southeastern Manitoba. Can J Zool 52:235–239

Lankester MW, Luttich S (1988) *Fascioloides magna* (Trematoda) in woodland caribou (*Rangifer tarandus caribou*) of the George River herd, Labrador. Can J Zool 66:475–479. doi:10.1139/z88-067

Lankester MW, Foreyt WJ (2011) Moose experimentally infected with giant liver fluke (*Fascioloides magna*). Alces 47:9–15

Leontovyč R, Košťáková M, Siegelová V, Melounová K, Pankrác J, Vrbová K, Horák P, Kašný M (2014) Highland cattle and *Radix labiata*, the hosts of *Fascioloides magna*. BMC Vet Res 10:1–7. doi:10.1186/1746-6148-10-41

Lorenzo M, Ramirez P, Mendez M, Alonso M, Ramos R (1989) Reporte de *Fascioloides magna*, Bassi, 1875, parasitando un wápiti (*Cervus canadensis*) en Cuba. Revista Cubana de Ciencias Veterinarias 20:263–266

Lydeard C, Mulvey M, Aho JM, Kennedy PK (1989) Genetic variability among natural populations of the liver fluke *Fascioloides magna* in white-tailed deer, *Odocoileus virginianus*. Can J Zool 67:2021–2025. doi:10.1139/z89-287

Majoros G, Sztojkov V (1994) Appearance of the large American liver fluke *Fascioloides magna* (Bassi, 1875) (Trematoda: Fasciolata) in Hungary. Parasit Hung 27:27–38

Marinculić A, Džakula N, Janicki Z, Hardy Z, Lučinger S, Živičnjak T (2002) Appearance of American liver fluke (*Fascioloides magna*, Bassi, 1875) in Croatia—a case report. Vet Arhiv 72:319–325

Marinković D, Kukolj V, Aleksić-Kovačević S, Jovanović M, Knežević M (2013) The role of hepatic myofibroblasts in liver cirrhosis in fallow deer (*Dama dama*) naturally infected with giant liver fluke (*Fascioloides magna*). BMC Vet Res 9:45. doi:10.1186/1746-6148-9-45

Maskey JJ (2011) Giant liver fluke in North Dakota moose. Alces 47:1–7

McClanahan SL, Stromberg BE, Hayden DW, Averbeck GA, Wilson JH (2005) Natural infection of a horse with *Fascioloides magna*. J Vet Diagn Invest 17:382–385. doi:10.1177/104063870501700415

Mulvey M, Aho JM (1993) Parasitism and mate competition: liver flukes in white-tailed deer. Oikos 66:187–192. doi:10.2307/3544804

Murray DL, Cox EW, Ballard WB, Whitlaw HA, Lenarz MS, Custer TW, Barnett T, Fuller TK (2006) Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monogr 166:1–30. doi:10.2193/0084-0173(2006)166

Novobilský A, Horáčková E, Hirtová L, Modrý D, Koudela B (2007) The giant liver fluke *Fascioloides magna* (Bassi 1875) in cervids in the Czech Republic and potential of its spreading to Germany. Parasitol Res 100:549–553. doi:10.1007/s00436-006-0299-4

Olsen OW (1949) White-tailed deer as a reservoir of the large American liver fluke. Vet Med 44:26–30

Peterson WJ, Lankester MW, Kie JG, Bowyer RT (2013) Geospatial analysis of giant liver flukes among moose: effects of white-tailed deer. Acta Theriol 58:359–365. doi:10.1007/s13364-013-0130-4

Pfeiffer H (1983) *Fascioloides magna*: Erster Fund in Österreich. Wien Tierarztl Monat 70:168–170 (in German)
Plötz C, Rehbein S, Bamler H, Reindl H, Pfister K, Scheuerle MC (2015) *Fascioloides magna*—epizootiology in a deer farm in Germany. Berl Munch Tierarztl Wochenschr 128:177–182. doi:10.2376/0005-9366-128-177
Pollock B, Penashue B, McBurney S, Vanleeuwen J, Daoust PY, Burgess NM, Tasker AR (2009) Liver parasites and body condition in relation to environmental contaminants in caribou (*Rangifer tarandus*) from Labrador, Canada. Arctic 62:1–12
Presidente PJA, McCraw BM, Lumsden JH (1980) Pathogenicity of immature *Fascioloides magna* in white-tailed deer. Can J Comparat Med 44:423–432
Price EW (1953) The fluke situation in American ruminants. J Parasitol 39:119–134
Pursglove SR, Prestwood AK, Ridgeway TR, Hayes FA (1977) *Fascioloides magna* infection in white-tailed deer of southeastern United States. J Am Vet Med Assoc 171:936–938
Pybus MJ (1990) Survey of hepatic and pulmonary helminths of wild cervids in Alberta, Canada. J Wildl Dis 26:453–459. doi:10.7589/0090-3558-26.4.453
Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames
Pybus MJ, Onderka DK, Cool N (1991) Efficacy of triclabendazole against natural infections of *Fascioloides magna* in wapiti. J Wildlife Dis 27:599–605
Pybus MJ, Butterworth EW, Woods JG (2015) An expanding population of the giant liver fluke (*Fascioloides magna*) in elk (*Cervus canadensis*) and other ungulates in Canada. J Wildl Dis 51:431–445. doi:10.7589/2014-09-235
Pyziel AM, Demiaszkiewicz AW, Kuligowska I (2014) Molecular identification of *Fascioloides magna* (Bassi, 1875) from red deer from south-western Poland (Lower Silesian Wilderness) on the basis of internal transcribed spacer 2 (ITS-2). Pol J Vet Sci 17:523–525. doi:10.2478/pjvs-2014-0077
Rajković-Janje R, Bosnić S, Rimac D, Gojmerac T (2008) The prevalence of American liver fluke *Fascioloides magna* (Bassi 1875) in red deer from Croatian hunting grounds. Eur J Wildl Res 54:525–528. doi:10.1007/s10344-007-0163-6
Rajský D, Patus A, Bielik J (1995) Záchyt cicavice obrovskej (*Fascioloides magna* Bassi, 1875) v rámci monitoringu bioty v oblasti Vodného diela Gabčíkovo. In: Kontrišová O, Kočík K, Bublinec E (eds) Zborník referátov, Monitorovanie a hodnotenie stavu životného prostredia. Technická univerzita, Zvolen (in Slovak)
Rajský D, Patus A, Špakulová M (1996) Rozšírenie cicavice obrovskej (*Fascioloides magna* Bassi, 1875) v jelenej chovateľskej oblasti J–I Podunajská. In: Zborník referátov a príspevkov medzinárodnej konferencie 1996. Výskumný ústav živočíšnej výroby, Nitra (in Slovak)
Rajský D, Čorba J, Várady M, Špakulová M, Cabadaj R (2002) Control of fascioloidosis (*Fascioloides magna* Bassi, 1875) in red deer and roe deer. Helminthologia 39:67–70
Rajský D, Dubinský P, Krupicer I, Sabo R, Sokol J (2006) Výskyt propagačných štádií *Fascioloides magna* a iných helmintov vo fekáliách jelenej zveri z okresov hraničiacich s riekami Dunaj a Morava. Slov Vet Čas 31:177–180 (in Slovak)
Rehbein S, Hamel D, Reindl H, Visser M, Pfister K (2012) *Fascioloides magna* and *Ashworthius sidemi*—two new parasites in wild ungulates in Germany. In: Program and abstracts of the XI European multicolloquium of parasitology (EMOP XI), Cluj-Napoca, Romania, 25–29 July 2012
Salomon S (1932) *Fascioloides magna* bei deutschem Rotwild. Berl Tierärztl Wochenschr 48:627–628 (in German)
Samuel WM, Low WA (1970) Parasites of the collared peccary from Texas. J Wildl Dis 6:16–23
Schillhorn van Veen TW (1987) Prevalence of *Fascioloides magna* in cattle and deer in Michigan. J Am Vet Med Assoc 191:547–548
Schwartz JE, Mitchell GE (1945) The Roosevelt Elk on the Olympic Peninsula, Washington. J Wildlife Manage 9:295–319. doi:10.2307/3796372
Schwartz WL, Lawhorn DB, Montgomery E (1993) *Fascioloides magna* in a feral pig. Swine Health Prod 1:27
Senger CM (1963) Some parasites of Montana deer. Montana Wildl Autumn:5–13

Severin K, Mašek T, Janicki Z, Konjević D, Slavica A, Marinculić A, Martinković F, Vengušt G, Džaja P (2012) Liver enzymes and blood metabolites in a population of free-ranging red deer (*Cervus elaphus*) naturally infected with *Fascioloides magna*. J Helminthol 86:190–196. doi:10.1017/S0022149X1100023X

Slavica A, Florijančić T, Janicki Z, Konjević D, Severin K, Marinculić A, Pintur K (2006) Treatment of fascioloidosis (*Fascioloides magna*, Bassi 1875) in free ranging and captive red deer (*Cervus elaphus* L.) at eastern Croatia. Vet Arhiv 76:9–18

Ślusarski W (1955) Studia nad europejskimi przedstawicielami przywry *Fasciola magna* (Bassi, 1875) Stiles, 1894. Acta Parasitol Pol 3:1–59 (in Polish)

Špakulová M, Čorba J, Varády M, Rajský D (1997) Bionomy, distribution and importance of giant liver fluke (*Fascioloides magna*), an important parasite of free-living ruminants. Vet Med 42:139–148

Steele E (2008) Prevalence of the large liver fluke, *Fascioloides magna*, in the white-tailed deer in South Carolina. In: Paper presented at the 4th annual USC upstate research symposium, University of South Carolina, Spartanburg, 11 April 2008

Stiles CW, Hassall A (1894) The anatomy of the large American fluke (*Fasciola magna*), and a comparison with other species of the genus *Fasciola*. J Comp Med Vet Arch 15:161–178, 225–243, 299–313, 407–417, 457–462. Cited in Pybus MJ (2001) Liver flukes. In: Samuel WM, Pybus MJ, Kocan AA (eds) Parasitic diseases of wild mammals, 2nd edn. Iowa State University Press, Ames

Swales WE (1935) The life cycle of *Fascioloides magna* (Bassi, 1875), the large liver fluke of ruminants, in Canada. Can J Res 12:177–215. doi:10.1139/cjr35-015

Ullrich K (1930) Über das Vorkommen von seltenen oder wenig bekannten Parasiten der Säugetiere und Vögel in Böhmen und Mähren. Prag Arch Tiermed 10:19–43 (in German)

Ursprung J, Prosl H (2011) Vorkommen und Bekämpfung des Amerikanischen Riesenleberegels (*Fascioloides magna*) in den österreichischen Donauauen östlich von Wien 2000–2010. Wien Tierarztl Monat 98:275–284 (in German)

Ursprung J, Joachim A, Prosl H (2006) Epidemiology and control of the giant liver fluke, *Fascioloides magna*, in a population of wild ungulates in the Danubian wetlands east of Vienna. Berl Munch Tierarztl Wochenschr 119:316–323 (in German)

Whiting TL, Tessaro SV (1994) An abattoir study of tuberculosis in a herd of farmed elk. Can Vet J 35:497–501

Winkelmayer R, Prosl H (2001) Riesenleberegel – jetzt auch bei uns? Österreichisches Weidwerk 3:42–44 (in German)

Wobeser BK, Schumann F (2014) *Fascioloides magna* infection causing fatal pulmonary hemorrhage in a steer. Can Vet J 55:1093–1095

Wobeser G, Gajadhar AA, Hunt HM (1985) *Fascioloides magna*: Occurrence in Saskatchewan and distribution in Canada. Can Vet J 26:241–244

Záhoř Z (1965) Výskyt velké motolice (*Fascioloides magna* Bassi, 1875) u srnčí zvěře. Veterinářství 15:329–324 (in Czech)

Záhoř Z, Prokeš C, Vítovec L (1966) Nález vajíček motolice *Fascioloides magna* (Bassi, 1875) a fascioloidózních změn v játrech skotu. Vet Med (Praha) 39:397–404 (in Czech)