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A MATHEMATICAL MODEL FOR THE ONTOGENY OF *FASCIOLA HEPATICA* IN THE DEFINITIVE HOST

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ABSTRACT: A mathematical model is developed for the biometric trajectory of *Fasciola hepatica* adult in experimentally infected laboratory albino rat. Lineal (mm) (body length BL, body width BW, perimeter P, cone body length CL, cone body width CW, distance between anterior end of body and acetabulum A-VS, distance between posterior end of body and acetabulum P-VS) and surface (mm²) (body surface BS, oral sucker surface OSS, ventral sucker surface VSS) measurements were analyzed. The measurements were made using software for image analysis. The model obtained for all the biometric characters as a function of time was logistic $y = y_m / [1 + z_0 \exp(-k a)]$, where y_m = the maximum value towards which the biometric character y tends, a = age, and z_0 and k are constants. Based on this model, if the variable time is eliminated, the following allometric function is obtained: $(y_{2m} - y_2) / y_2 = c [(y_{1m} - y_1) / y_1]^b$, where y_1 = BS or BL, y_{1m} is the maximum value towards which y_1 tends, y_2 = one of the biometric characters analyzed, y_{2m} is the maximum value towards which y_2 tends, and c and b are constants. The allometric function obtained is applied to a natural cattle-parasitizing population, better fits being observed than with the classic allometric equation $y = cx^b$.

KEY WORDS: *Fasciola hepatica*, biometry, adult, logistic law, albino rat, cattle.

INTRODUCTION

The development and maturation of the adult stage of the liver fluke *Fasciola hepatica* Linnaeus, 1758 (Trematoda: Fasciolidae) in the definitive host has been the subject of not so many studies. The most important papers referring to the development of the different large structures and teguments of this digenean species are those of DAWES (1962 a, b, c), DAWES & HUGHES (1964), KUBLITSKENE (1963), PANTELOURIS (1965), BENNETT & THREADGOLD (1973, 1975), and BENNETT (1977). However, there is no detailed study concerning the changes in the quantitative characteristics of the adult worm during its development.

In a developing organism, magnitudes associated to structures change according to growth laws. These magnitudes can be plotted against time, the resulting graphs being defined as their ontogenetic trajectories. The latter have their analytical counterpart solutions in differential equations expressing growth rules. Thus, the ontogenetic trajectory of a given parameter is established by its relation to time, which can only be applied when working with experimentally reared populations (VALERO, DE RENZI & MAS-COMA, 1991).

When studying natural populations, only the allometric growth of a given biometric parameter as a function of another biometric parameter can be calculated. In this case, the classic allometry equation described by HUXLEY (1972) is usually used, though other allometry functions from growth laws can be proposed. However, Huxley's equation involves the inconvenience of supposing unlimited growth, which in general is unrealistic for digenean trematodes (VALERO, DE RENZI & MAS-COMA, 1991).

The laboratory albino rat, *Rattus norvegicus*, is well known and widely used as an experimental host for the liver fluke. Curiously, and despite the suitability of this rodent host for drug screening tests and immunological studies (see review by BORAY, 1969), the ontogenetic trajectories of *F. hepatica* adult characteristics in the albino rat have never been the subject of a specific study. Such a study, and the development of an approach to allometric analyses in this parasite is the aim of the present paper. Allometries result from differential growth rates, which can be constant (exponential growth rules) or variable (logistic or saturated rules). When all the growth stages are available, allometric curves have a specific shape according to their underlying growth rules. Since growth rules cannot be inferred from natural populations, estimation of the allometry parameters can supply information about them. Allometries according to saturated or logistic laws are easily characterized by their graphic plots; limit biometric characters are present in their expression, and so they can be estimated in consequence. An iterative trial method similar to that proposed by DE RENZI (1988) is used to estimate such limit biometric characters. Thus, some light can be cast on the unknown ontogenetic trajectories. In this case, allometry will be inferred in two ways for an experimental population: a) from the estimated biometric characters of the ontogenetic trajectories, and b) from the raw data without any time measurement. A comparison of results will be carried out. In a subsequent step, the second procedure will be applied to a natural population of *F. hepatica* from Corsican cattle.

MATERIAL AND METHODS

Material

Experimentally obtained parasites: *F. hepatica* metacercariae were obtained from experimentally infected *Lymnaea truncatula*.

Only 1-12 day-old metacercariae were used. They were stored at 4 C until required. Before given to rats, their viability was checked using the refractile appearance of the excretory granules as a criterion. The molluscan intermediate host, *L. truncatula*, shedding the cercariae which gave rise to the metacercariae, were from a laboratory-reared (in climatic chambers Heraeus-Vötsch HPS 1500 & HPS 500; experimental conditions: temperature 20° C; photoperiod 12 h/12 h light/darkness; r.h. 90%) strain originating from the Mediterranean island of Corsica. These snails were, in turn, monomiracidially infected with *F. hepatica* eggs found in bile from naturally infected cattle killed in the slaughter-house of Portovecchio (Corsica, France).

Experimental animal host: Wistar rats (Iffa Credo, Barcelona, Spain) were used throughout. Animals were housed in Micro-Isolator boxes (Iffa Credo, Barcelona, Spain) and maintained in a pathogen-free room, electrically heated with a 12 h/12 h light/darkness cycle (conditions according to the European Agreement of Strasbourg, 18 March 1986). Food and water were available *ad libitum*.

Experimental design: A total of 12 males and 6 females of 2-3 month-old albino rats were infected with 20 *F. hepatica* metacercariae per rat. The number of worms which successfully developed in each rat was established by dissection (see Table 1). Metacercariae were inoculated orally by means of paper pellets under controlled ether anesthesia (Panreac, Barcelona, Spain). Albino rats were divided into 5 groups according to 5 different postinfection periods (equal to the age of the parasite adult stage): 30, 40, 50, 75 and 100 days. At the given times, the rats were sacrificed with ether anesthesia and *F. hepatica* worms were collected under a dissecting microscope. Initially the bile duct was examined for the presence of worms. Afterwards, the thoracic and abdominal viscera and cavities were examined and thoroughly rinsed with water to assure the recovery of all worms (see Table 1). The sample size obtained was 11 adults. The detection of eggs in faeces was carried out by the Kato-Katz technique (Helm-Test®, Belo Horizonte, Brazil).

Parasites of natural origin: A total of 125 *F. hepatica* adults were obtained from naturally parasitized bile ducts of Corsican cattle (*Bos taurus*) in different localities on the island of Corsica (France).

Methods and techniques

Fixation, staining and mounting techniques: Both the experimental adult specimens and those corresponding to natural parasitation were fixed with Bouin's solution between slide and coverglass (but without coverglass pressure), stained with Grenacher's borax carmine and mounted in Canada balsam (Panreac, Barcelona, Spain).

Measurement techniques and data analyses: All measurements were made according to the method proposed by MAS-COMA, MONTOLIU & VALERO (1984) for Brachylaimidae Trematoda adults, but modified by us for Fasciolidae. Fig. 1 shows the measurements of organs and body proportions studied: a) Lineal measurements (mm): body length (BL), body width (BW), perimeter (P), cone body length (CL), cone body width (CW), distance between anterior end of body and acetabulum (A-VS), distance between posterior end of body and acetabulum (P-VS); b) Surfaces (mm^2): body surface (BS), oral sucker surface (OSS), ventral sucker surface (VSS); c) relations: relation between sucker surfaces (OSS/VSS). The measurements were made using image analysis software (Vidas-Videoplan, Karl-Zeiss).

The logistic model: The relationship between the biometric characters and time was analyzed. The mathematical approach adopted was that of ALBERICH *et al.* (1979) and VALERO, DE RENZI & MAS-COMA (1991). Data processing was carried out with Cricket and SSPS software (Macintosh). Adjusted non lineal curves were tested using r^2 and the least-squares residual (sse).

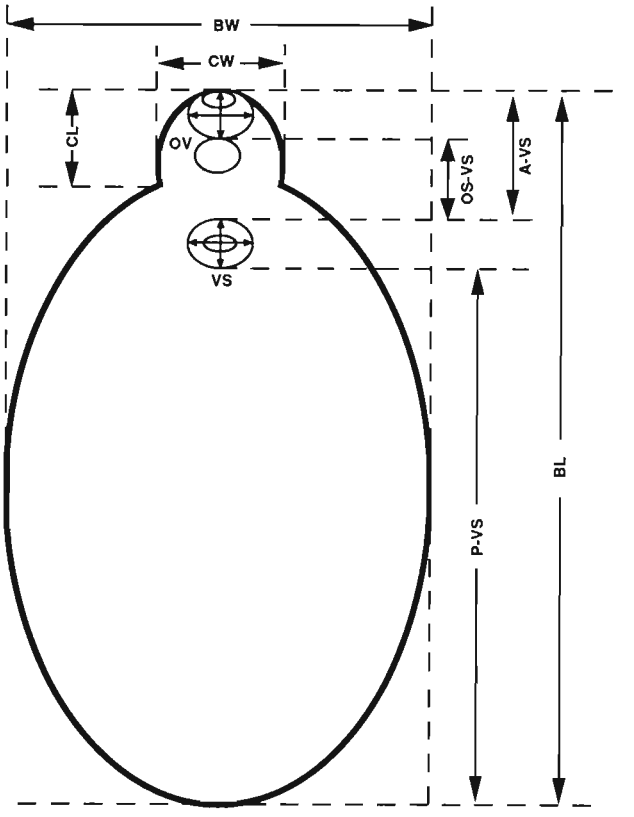

Fig. 1.– Standardized measurements in *Fasciola hepatica* adult.

The relationship between a parameter y and age a may be estimated by the logistic law:

$$dy/da = k\, y\, (1 - y / y_m) \qquad [1]$$

where k is a geometric rate of increase and y_m the limit of y. In the solution of this equation, y approaches y_m as a increases.
The integration of [1] yields the ontogenetic trajectory

$$y = y_m / [1 + z_o\, exp\, (-k\, a)] \qquad [2]$$

Allometry: The relationship between y_1 and y_2 cannot be estimated by the classical allometric expression, in this case

$$(y = cx^z) \qquad [3]$$

In the logistic model z's follow this relationship, and by replacing z's for their values, we obtain

$$(y_{2m} - y_2) / y_2 = c\, [(y_{1m} - y_1) / y_1]^p \qquad [4]$$

In laboratory obtained parasites, growth can be chronologically controlled and consequently the age measurement equals time (absolute age is unknown), as a result of which selected parameters must be used as relative ages (VALERO, DE RENZI & MAS-COMA, 1991). In the present paper body length (BL) and body surface (BS) have been selected as age measurements for the natural popu-

lation, taking into account the general adult stage morphology of *F. hepatica*.

A problem arises when natural populations are investigated, as the developmental time control formula [2] is not available for absolute time. Since formula [4] contains the y_m assymptotic values, one procedure consists of simultaneously attempting successive values for y_{1m} and y_{2m}. In the present case, the results exhibit good agreement. Allometric parameters will be inferred from [2]: b is the ratio k_2 / k_1, whereas c is z_{m2} / z_{m1}^b.

As applied for Trematodes in general, the analyses of allometric growth patterns of the flukes have been performed according to the Huxley's 1932 classic allometric formula (HUXLEY, 1972)

$$y = cx^a \qquad [3]$$

where y = organ size, x = body size, b = allometric exponent and c is a constant. When $b = 1$, the two variables have similar growth rates. When a is either greater or smaller then 1, the body proportion or organ is considered to be positive or negative in allometric growth, and exhibits a higher or lower growth rate than body size.

RESULTS

Susceptibility in the albino rat

The liver parenchyma of infected rats presented migratory worms within 30 days. Infection was confined to the principal bile duct from the 40 days group. Table 1 summarizes the results of the experimental infections. A total of 11 worms (1-3/host, mean = 1,6) were found in the livers of 7 albino rats fed 20 cysts each, with an infectivity of 38,8% [(number of rats positive to infestation) / total number of rats)×100] (33,3% in male and 50% in female hosts). The percentage of worms recovered [(flukes recovered) / (cysts administered)×100] was 3% (2% in male and 4% in female hosts). The prepatent period was very consistent in all animals, ranging from

Rat sex	Rat age (months)	Worm age (days)	Worms recovered	% worms recovered	Micro-habitat	Met. age (days)
M	2	30	1	5%	LP	8-12
F	2	30	1	5%	LP	8-12
M	2	40	1	5%	LP	8-12
M	3	40	3	15%	PBD	4-8
M	2	50	1	5%	PBD	8-12
F	2	75	2	10%	PBD	1-4
F	2	100	2	10%	PBD	1-4

Table 1.– Results obtained in the study of albino rat infestation with *Fasciola hepatica*. M = male; F = female; LP = liver parenchyma; PBD = principal bile duct; Met. = metacercariae.

	30 days n = 2	40 days n = 4	50 days n = 1	75 days n = 2	100 days n = 2
BS	7,832-9,053	9,550-17,490	42,580	85,440-87,330	90,920-109,10
(mm²)	(8,443)	13,520)		(86,385)	(100,010)
BL	5,281-5,346	5,954-8,046	10,970	14,320-14,320	15,360-16,550
(mm)	(5,314)	(7,000)		(14,320)	(15,955)
BW	2,097-2,455	2,264-2,988	5,545	8,556-9,147	8,650-9,691
(mm)	(2,276)	(2,609)		(8,852)	(9,171)
P	12,040-12,460	13,470-18,190	26,390	36,280-36,370	37,710-41,170
(mm)	(12,250)	(15,838)		(36,325)	(39,440)
CL	0,973-1,260	1,145-1,288	1,432	1,775-1,976	1,775-2,004
(mm)	(1,117)	(1,217)		(1,876)	(1,890)
CW	1,174-1,260	1,231-1,346	1,976	2,291-2,663	2,291-2,864
(mm)	(1,217)	(1,302)		(2,477)	(2,577)
ø max OSS	0,372-0,458	0,315-0,372	0,544	0,572-0,658	0,572-0,601
(mm)	(0,415)	(0,343)		(0,615)	(0,587)
ø min OSS	0,257-0,315	0,229-0,864	0,486	0,458-0,458	0,458-0,544
(mm)	(0,286)	(0,264)		(0,458)	(0,501)
OSS	0,037-0,092	0,053-0,151	0,149	0,361-0,736	0,483-0,568
(mm²)	(0,065)	(0,085)		(0,548)	(0,525)
ø max VSS	0,429-0,486	0,486-0,572	0,658	0,859-0,859	0,973-0,973
(mm)	(0,458)	(0,529)		(0,859)	(0,973)
ø min VSS	0,400-0,429	0,486-0,544	0,687	0,773-0,801	0,838-0,838
(mm)	(0,415)	(0,515)		(0,787)	(0,838)
VSS	0,131-0,269	0,219-0,326	0,381	0,480-1,326	0,724-1,013
(mm²)	(0,200)	(0,264)		(0,903)	(0,869)
A-VS	1,059-1,202	1,116-1,288	1,718	0,941-1,722	1,221-1,531
(mm)	(1,131)	(1,356)		1,331)	(1,376)
VS-P	3,646-3,858	4,382-4,611	8,678	11,799-12,115	12,974-13,604
(mm)	(3,752)	(4,477)		(12,859)	(13,289)
OS/VS	0,139-0,702	0,178-0,581	0,390	0,272-1,532	0,560-0,667
	(0,420)	(0,380)		(0,902)	(0,613)

Table 2.– Evolution of the biometric parameters of *Fasciola hepatica* in the albino rat according to age (in days); all values shown as range and mean in parentheses. n = numbers of adults.

	y_m	$-k \pm$ S. E.	z_o	r^2	sse
BS	109,2	0,081 ± 0,011	114,74 ± 73,607	0,98	111,136
BL	16,56	0,063 ± 0,008	14,469 ± 4,950	0,98	1,156
BW	9,2	0,094 ± 0,019	76,921 ± 63,556	0,98	0,934
P	41,0	0,068 ± 0,009	19,466 ± 7,672	0,99	8,135
CL	2,0	0,045 ± 0,007	3,393 ± 1,080	0,97	0,017
CW	2,7	0,058 ± 0,012	8,106 ± 4,130	0,96	0,067
OSS	0,570	0,070 ± 0,016	112,080 ± 186,600	0,97	0,006
VSS	1,015	0,070 ± 0,016	46,305 ± 38,114	0,95	0,002
A-VS	1,835	0,078 ± 0,029	7,477 ± 8,163	0,87	0,052
VS-P	13,6	0,085 ± 0,015	45,747 ± 30,995	0,98	1,708

Table 3.– Fasciola hepatica in the albino rat: changes in the biometrical variables as a function of time in the logistic model $y = y_m / [1 + z_o \exp(-k\,a)]$ [see 2]. r^2 = adjusted; sse = least-squares residual.

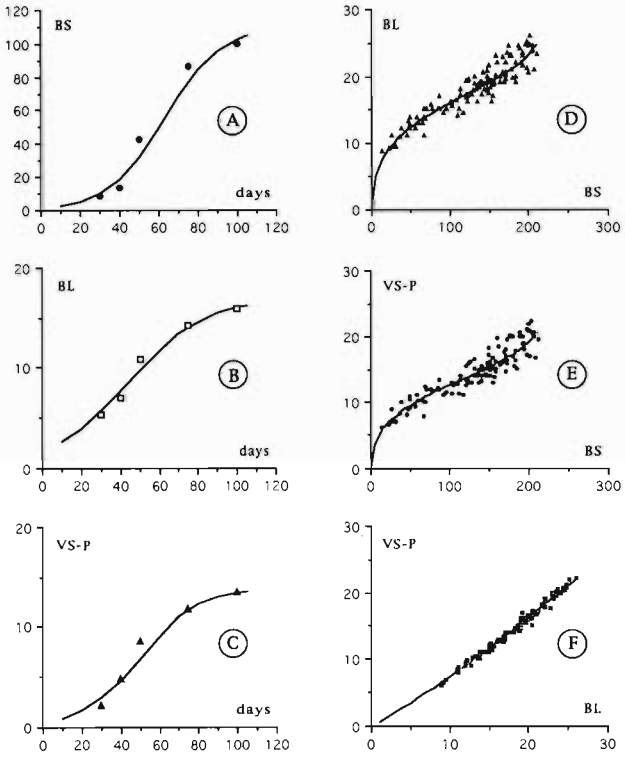

Fig. 2.– A, B, C) Ontogenetic trajectories obtained in *Fasciola hepatica* from experimental adults in albino rat; each point represents the mean in each age class; changes in body surface (A), body length (B), and distance between acetabulum and posterior body (C) as a function of days post-infestation following the logistic model $y = y_m / [1 + z_o \exp(-k\,a)]$; D, E, F) allometric model $(y_{2m} - y_2) / y_2 = c\,[(y_{1m} - y_1) / y_1]^b$ obtained in *F. hepatica* from natural adults in cattle; each point represents an individual adult; changes in body length as a function of body surface (D), distance between acetabulum and posterior body as a function of body surface (E), and distance between acetabulum and posterior body as a function of body length (F).

41 to 51 days (mean = 45,2). It must be added here that whereas the number of adult worms recovered in successfully infected rats enters perfectly within the normal range usually obtained in experimental infections of rats with *F. hepatica* metacercariae, the very low number of rats which became infected may be explained because of the negative effects of the ether anesthesia applied at the moment of the infestation. Although this negative effect was already known before, the decision to carry it this way was obliged because of the necessity to obtain significant compared results with similar infection experiments with wild black rats, a host species which enables no other experimental infection method.

Growth and development in the albino rat

Individual measurements by age groups are shown in Table 2. The ontogenetic trajectories of all the parameters have been studied. All data but A-VS (Table 3, Fig. 2 A, B, C) fit the sigmoidal model well [see 2]. The r^2 values for all measurements but A-VS were very high.

The body growth and development of *F. hepatica* in the albino rat were characterized as follows. The «exponential» part of logistic growth is associated to body development and sexual maturation, which take place during migration in the abdominal cavity, the liver parenchyma and the entry of flukes to the biliary duct system. The pattern of development of the flukes in the albino rat in this period is: a) gonadal differentiation (evident by day 40); b) eggs in the uterus and oviposition (by days 40-50); c) growth persisting considerably after sexual maturity, followed by gradually stationary growth thereafter (Fig. 2 A, B, C).

Application of the function to populations in nature

The morphometric values of *F. hepatica* parasitizing *B. taurus* (Corsica) are shown in Table 4. Table 5 in turn compares the fit of the two models for each biometrical variable as a function of BS and BL. This Table shows that the logistic model [4] (Fig. 2 D, E, F) fits better than the exponential model [3] (compare sse column for each model; sse values corresponding to the logistic model are lower than those corresponding to the exponential model) in BL, VS-P a function of BS and VS-P a function of BL. Table 5 also provides r^2. Parameters BL, P, and VS-P as a function of BS, and BW, P,

	range mean ± S.E.
BS	13,800-212,000
(mm^2)	(128,486 ± 5,505)
BL	8,900-26,000
(mm)	(17,773 ± 0,427)
BW	3,100-12,500
(mm)	(8,939 ±0,231)
P	23,020-118,500
(mm)	(68,341 ± 2,747)
CL	1,174-2,949
(mm)	(2,217 ± 0,035)
CW	1,546-3,580
(mm)	(2,767 ± 0,046)
OSS	0,176-0,618
(mm^2)	(0,412 ± 0,010)
VSS	0,244-1,636
(mm^2)	(0,830 ± 0,021)
A-VS	1,116-3,007
(mm)	(2,308 ± 0,041)
VS-P	6,100-22,300
(mm)	(14,284 ± 0,396)

Table 4.– Morphometric data of the *Fasciola hepatica* population from *Bos taurus* (Corsica): all values shown as range and mean ± S.E. in parentheses. S.E. = standard error; n = 125.

and VS-P as a function of BL are statistically significant ($P < 0,05$).

DISCUSSION

Ontogenetic trajectories

Close comparison of growth data with those obtained in other studies on digenean parasites is difficult in the majority of cases because of the different fixation technique used (LAGRANGE & GUTMANN, 1961) or the presence of only the growth curves in the papers, the absence of sufficient raw data making a mathematical verification of the growth pattern impossible (CLEGG, 1965; KINSELLA, 1971; BOURNS, ELLIS & RAU, 1973; SCHUSTER & LÄMMLER, 1973; SAITO, 1984; POITOU, BAEZA & BOULARD, 1993).

Concerning the family Fasciolidae, data furnished by FOREYT & TODD (1976) concerning *Fascioloides magna* (Bassi, 1875) in deer follow a logistic growth pattern. The growth model of adult *F. hepatica* is apparently sigmoidal in experimental sheep models in light infections (BORAY, 1969), and in rodent models (albino rat and mouse) (DAWES, 1962 a, b; THORPE, 1965; BORAY, 1969) (see Fig. 3). According to these authors, growth is remarkably uniform after the first week of development in mice and in rat, whereas the growth rates in rabbits and guinea-pigs during the early phases of development are less.

Allometric growth

The results obtained regarding the allometry of adult *F. hepatica* in micro- and macro-mammals reveal different maximum values of y_m. This observation indicates that the growth of *F. hepatica* is influenced by the nature of the definitive host, the size of the parasitation microhabitat therefore representing a growth limiting factor. However, it must be taken into account that adult fluke architectural constitution also imposes limits on growth.

Allometric growth according to Huxley's 1932 function in Digenetic Trematodes has been studied by THOMAS (1965) for *Mesocoelium monodi* Dollfus, 1929 (Mesocoeliidae), FISCHTHAL & KUNTZ (1967) for *Pleurogenoides taylori* (Tubangui, 1929)(Pleurogenidae), MARTIN (1969) for *Castroia amplicava* Travassos, 1928 and *C. silvai* Travassos, 1928 (Lecithodendriidae), FISCHTHAL (1978) for *Apocreadium mexicanum* Manter, 1937 (Apocreadiidae), *Pseudocreadium lamelliforme* (Linton, 1907) (Lepocreadiidae) and *Paracryptogonimus americanus* Manter, 1940 (Cryptogonimidae), FISCHTHAL, FISH & VAUGHT (1980), FISCHTHAL, CARSON & VAUGHT (1982 a, b) for *Bucephalus gorgon* (Linton, 1905) (Bucephalidae) and *Lissorchis attenuattus* (Monorchiidae) respectively, ROHDE (1966) for *Anchitrema sanguineum* (Sonsino, 1894) (Dicrocoeliidae), BETTERTON & LIM (1977) for *Skrjabinus* sp. and *Zonorchis* sp. (Dicrocoeliidae), WIRORENO, CARNEY & ANSORI (1987) for *Eurytrema pancreaticum* (Janson, 1889) (Dicrocoeliidae) and SWARNAKUMARI & MADHAVI (1992) for *Philophthalmus nocturnus* Looss, 1907 (Philophthalmidae). OSHIMA, AKAHANE & SHIMAZU (1968) and AKAHANE, HARADA & OSHIMA (1974) applied Huxley's equation to *Fasciola* sp. from Japan, for the distance between the anterior end of the body and the middle of the ventral sucker/body length, and body width/body length; negative allometry was obtained, with positive allometry for body weight/body length.

In all above mentioned digenean species the results of allometric growth studies are essentially similar. The hind body proves to be positive, with a posterior-anterior growth gradient. THOMAS (1965) further suggested that this phenomenon is due to the uterus growing at a rate faster than the rest of the body. He indicated that this argument is not applicable to *F. hepatica* as it has a short preacetabular uterus, and suggested that the posterior-anterior growth gradient is not directly dependent on uterine growth but perhaps represents a general phenomenon shared by other digenetic trematodes. We consider that the positive allometry of the hind body possibly reflects an increase in the surface of the digestive system, with a corresponding increase in the absorptive surface. Our results in the *F. hepatica* populations analyzed in rats and cattle with Huxley's equation were identical. The posterior growth gradient was confirmed by the positive allometry detected in VS-P/BL.

Several studies have shown that allometric growth of body parts and organs of trematodes can also be influenced by: a) host species (FISCHTHAL, FISH & VAUGHT, 1980); b) intensity of infection in the same species (FISCHTHAL, CARSON & VAUGHT, 1982 a); c) site of infection in a host (FISCHTHAL, CARSON & VAUGHT, 1982

y_1	y_2	y_{1m}	y_{2m}	b ± S.E.	c ± S. E.	r^2	F	sse
				logistic model				
BS	BL	213	26,2	0,544 ± 0,025	0,593 ± 0,016	0,87	264,852	199,162
BS	BW	–	–	–	–	–	–	–
BS	P	213	118,8	0,628 ± 0,059	0,992 ± 0,065	0,66	3,500	22348,296
BS	CL	–	–	–	–	–	–	–
BS	CW	–	–	–	–	–	–	–
BS	OSS	–	–	–	–	–	–	–
BS	VSS	–	–	–	–	–	–	–
BS	A-VS	–	–	–	–	–	–	–
BS	VS-P	213	22,4	0,057 ± 0,028	0,728 ± 0,023	0,85	216,625	204,701
BL	BW	26,2	12,6	1,152 ± 0,111	0,849 ± 0,064	0,60	47,784	191,331
BL	P	26,2	118,8	1,140 ± 0,094	1,800 ± 0,147	0,74	109,991	17047,193
BL	CL	–	–	–	–	–	–	–
BL	CW	–	–	–	–	–	–	–
BL	OSS	–	–	–	–	–	–	–
BL	VSS	–	–	–	–	–	–	–
BL	A-VS	–	–	–	–	–	–	–
BL	VS-P	26,2	22,4	1,015 ± 0,015	1,240 ± 0,015	0,98	5108,034	16,672
				classical allometric model				
BS	BL	–	–	0,451 ± 0,022	2,038 ± 0,223	0,85	661,181	232,145
BS	BW	–	–	0,477 ± 0,023	0,906 ± 0,107	0,86	901,828	65,920
BS	P	–	–	0,711 ± 0,068	2,204 ± 0,755	0,65	247,024	22977,541
BS	CL	–	–	0,188 ± 0,023	0,904 ± 0,105	0,37	90,040	8,331
BS	CW	–	–	0,223 ± 0,023	0,954 ± 0,108	0,53	124,951	8,714
BS	OSS	–	–	0,265 ± 0,045	0,115 ± 0,025	0,31	42,491	0,649
BS	VSS	–	–	0,201 ± 0,046	0,318 ± 0,072	0,19	22,027	3,214
BS	A-VS	–	–	0,249 ± 0,023	0,704 ± 0,081	0,59	147,614	6,042
BS	VS-P	–	–	0,529 ± 0,029	1,121 ± 0,164	0,83	549,629	238,094
BL	BW	–	–	0,789 ± 0,074	0,929 ± 0,205	0,59	185,987	195,190
BL	P	–	–	1,457 ± 0,101	1,013 ± 0,308	0,74	351,292	17086,170
BL	CL	–	–	0,416 ± 0,050	0,673 ± 0,099	0,44	84,169	6,152
BL	CW	–	–	0,475 ± 0,049	0,709 ± 0,103	0,51	110,328	9,114
BL	OSS	–	–	0,572 ± 0,093	0,079 ± 0,021	0,31	42,831	0,649
BL	VSS	–	–	0,347 ± 0,100	0,307 ± 0,090	0,12	13,991	3,490
BL	A-VS	–	–	0,514 ± 0,051	0,529 ± 0,079	0,54	119,673	6,698
BL	VS-P	–	–	1,162 ± 0,014	0,501 ± 0,021	0,98	8184,906	16,972

Table 5.– Comparison between the logistic $(y_{2m} - y_2) / y_2 = c\,[(y_{1m} - y_1) / y_1]^b$ [see 4] and the classic allometric $y = cx^b$ [see 3] models in *Fasciola hepatica* adults from Corsican cattle. *b, c* = constants that appear in both models; r^2 = adjusted; y_m = maximum value of biometric character in the logistic model; sse = least-squares residual in both models.

b); d) competitive inhibition among flukes (THORPE, 1965); e) the crowding effect (THORPE, 1965); f) age resistance and host reaction in hosts previously infected (HAYES, BAILER & MITROVIC, 1972, 1973, 1974; RAJASEKARIAH & HOWELL, 1977).

NEUHAUS (1978) considered that the application of Huxley's equation to Digenetic Trematodes is limited, due to the existence of diminished growth in the late stages of development. Studies by this author on the uterine allometry in *Dicrocoelium dendriticum*, *Pleurogenoides medians* and *F. hepatica* regarding body size (length of the uterus of all three species at different stages of development/body size) apply a modification of Huxley's growth law: $y = ax + a\,(xw + x)^2 + b$ (where y = log length of the uterus, x = log body length, and xw = log body length at the turning point).

The use of the logistic model provides information on the intraspecific variability of natural populations of *F. hepatica* adult. In this sense, the proposed growth model may be applied to further studies involving different approaches to the evaluation of the factors which influence trematode growth, as well as to health measures including host control, chemotherapeutics, the efficacy of vaccines, and so on.

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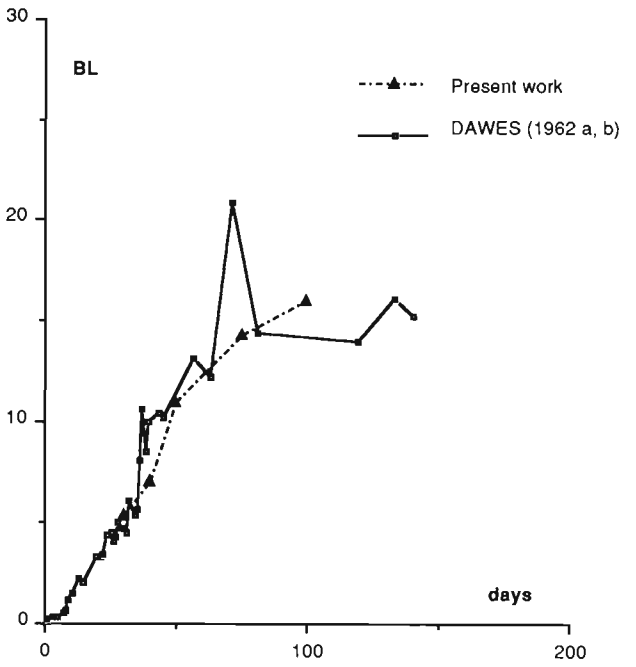

Fig. 3.– Comparison of the evolution of body length (BL) of *Fasciola hepatica* over time obtained in albino rat in the present study and those reported by DAWES (1962 a,b) in the mouse.

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