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THE STABILITY OF THE CAT AND DOG STRAINS OF *ANCYLOSTOMA CANINUM**

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When investigations upon hookworm disease in dogs were begun by this laboratory in 1925, a strain of *Ancylostoma caninum* Erc. was obtained for experimental use from a naturally infected dog in Baltimore. The first of a long series of studies upon the biology of this parasite was made by Herrick (1928) and this was followed closely by Scott's (1928) study of the development of this species in normal and abnormal hosts. Among other results of these studies was the observation that this strain of the dog hookworm was able to reach sexual maturity in *both* cats and dogs, but that the former was a highly refractory host in which, at best, only a small percentage of a given dose of infective larvae was able to survive.

Meanwhile (Sept., 1925), a cat obtained from Cold Spring Harbor, Long Island, was autopsied and found to harbor 10 specimens of *A. caninum.* Larvae were cultured from the contents of the rectum and administered to a young dog, in which host they showed "a peculiar lack of infectivity" (Scott, 1929, p. 209). On the other hand, this strain was readily perpetuated in cats. In subsequent experiments, Scott (1929, 1929a) was able to demonstrate that he was dealing in these cases with physiologically different strains which were especially adapted to the dog and to the cat.

An evaluation of the data of this report necessitates a summary consideration of the quantitative infectivity of these strains in cat and dog hosts. The behavior of the dog strain in dogs has been especially well studied during years of experimental hookworm work in this laboratory, yet it has seemed advisable for the present purpose to consider only those data which were obtained under exactly parallel conditions, where, for example, larvae from the same culture were tested at the same time in both hosts. Such data have been presented by Scott (1929), McCoy (1931), and Foster and Cort (1932), and, in passing over the individual results obtained, it should be stated that the findings by each author were essentially the same. The summarized comparative data upon the infectivity of these strains is as follows, where the percentages represent the average proportion of infective larvae which reached maturity in young

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hosts, and the figures in parentheses are the number of animals which were tested:

	In dogs	In cats
Dog strain	55.0% (9)	2.3% (21)
Cat strain	0.5% (16)	33.0% (21)

It has seemed from these data that the dog strain is better adapted to the dog host than is the cat strain to the cat host, and that cats in general are more susceptible to infection with the dog strain than are dogs with the cat strain. But the most important conclusion is that both strains are highly infective to their respective hosts and only slightly so to the opposite host.

Perhaps the most significant observation upon the stability of these strains was made by Scott (1930). He noted that the dog strain retained its infectivity for dogs and did not become more infective to cats, even after three successive generations in the cat host. On the other hand, in a single experiment where the cat strain was passed through the dog host, a higher infectivity was obtained in one dog (20 per cent) than in one cat (5 per cent). This apparently reversed infectivity of the cat strain, after a single generation in the dog host, caused both Scott (1930a, p. 89) and McCoy (1931, p. 200) to lament the absence of further information upon that point, since its confirmation would lead to many interesting considerations with respect to several other parasites of both medical and veterinary importance. These were the reasons for making the observations contained in this report. The same physiological strains of *A. caninum* were employed and relatively young animals were used throughout.

OBSERVATIONS AND DATA

Over a period of about two years, the cat strain was passed through nine successive generations of dog and cat hosts, and its infectivity noted at each stage. The data and host passages are presented in Table 1 and Chart 1.

As a starting point, infective larvae were cultured from eggs passed by D 642, which had been infected by McCoy (1931, p. 197) with 6,600 larvae of the straight cat strain. It became positive to Lane examinations in 17 days and was autopsied on the 34th day. Six worms were recovered, giving a development of 0.1 per cent, which is very typical of the development of this strain in dogs.

Larvae cultured from eggs passed by D 642 were given to 2 dogs and 1 cat (Table 1, A). Both dogs began passing eggs after periods of 15

TABLE I.—*Infectivity of the cat strain of* A. caninum *after varying numbers of passages through dog and cat hosts*

Larvae from	Given to	Days, infection to autopsy	Larvae given	Worms recovered	% development in dogs	% development in cats
A. Infectivity after 1 generation in a dog						
D 642	D 646	31	532	430	80.80	
	C 472(a)	31	1,600	0		0.00
	D 652	28	266	82	30.90	
B. Infectivity after 2 generations in dogs						
D 646	D 658	28	280	134	48.00	
	C 480(a)	25	20,000	0		0.00
	C 484(b)	7	20,000	700(?)		3.50
D 652	C 483	52	20,000	107		0.53
	C 479	28	20,000	19		0.09
	D 665	29	200	149	74.50	
C. Infectivity after 3 generations in dogs						
D 665	D 664	Not autopsied	325	—	—	
	C 496(b)	49	7,200	2		0.03
	C 497(a)	49	7,200	0		0.00
	C 512	47	6,000	5		0.08
C₁. Infectivity after 2 generations in dogs and 1 in a cat						
C 483	D 666	15	2,000	918	45.50	
	D 695(b)	12	1,000	870	87.00	
	C 508(a)	21	2,000	997		49.85
	C 514	54	1,000	5		0.50
	C 511	54	500	9		1.80
D. Infectivity after 2 generations in dogs and 2 in cats						
C 511	C 513(b)(d)	51	685	1		0.15
	C 518(c)(d)	156	1,000	0		0.00
	C 519(d)	40	1,350	152		11.26
	C 520(d)	19	1,350	244		18.10
	D 687	40	700	243	34.80	
E. Infectivity after 2 generations in dogs and 4 in cats						
C 518	C 516(a)(d)	21	11,000	0		0.00
	C 523(a)(d)	21	1,000	0		0.00
	C 524(a)	21	11,000	0		0.00
	C 525(a)	21	1,000	0		0.00
	C 534	82	1,000	8		0.80
	C 535(c)	61	1,000	0		0.00
	C 536(b)	19	750	80		10.70
	C 537(b)	10	750	180		24.00
F. Infectivity after 2 generations in dogs and 4 in cats						
C 534	C 550	165	7,000	5		0.07
	C 551	31	7,000	57		0.81
	C 552	32	7,000	28		0.40
G. Infectivity after 2 generations in dogs and 5 in cats						
C 550	C 570	121	2,020	337		16.68
	C 573	29	1,720	638		37.09
H. Infectivity after 2 generations in dogs and 6 in cats						
C 570	C 577(b)	27	2,000	998		50.00
	C 579(b)	28	2,000	1,100		55.00
	C 553(b)	12	77,000	2,600		3.38
	D 728(a)	32	2,000	0	0.00	

(a) Negative throughout to Lane examinations and negative at autopsy.
(b) Negative throughout to Lane examinations but worms present at autopsy.
(c) Positive to Lane examinations earlier, but worms lost before autopsy.
(d) Starved 2–2½ weeks during interval between infection and autopsy.

and 18 days, respectively, while the cat remained negative. At autopsy on the 28th day, one dog (D 652) yielded 82 worms, this representing about 31 per cent development. The other two animals were autopsied 3 days later, and no worms had matured in the cat, while in the dog (D 646) a better development (81 per cent) obtained than has usually occurred in instances where the straight dog strain has been used. This repetition of Scott's (1930, p. 151, Table 1, D) experiment, therefore, gave even stronger support for his original hypothesis than did his own data. It does appear, then, that the cat strain loses in infectivity for cats and becomes highly infective to dogs (simulating the straight dog strain) after passage through the dog host. Scott's figure of 5 per cent for the development of this strain in one cat, under similar conditions, is probably high, although it need not be accounted for by individual variation in host-susceptibility, since this cat was autopsied only 20 days after infection, and as shall be clear from the data to follow there is a great loss of worms from the more refractory hosts just before sexual maturity is reached.

For the next generation, the strain was continued from each dog into 2 cats and 1 dog (Table 1, B). More cats were employed as well as larger larval doses, in order to insure, if possible, the resumption of the strain from the cat host. Both dogs (D 658 and D 665) developed good

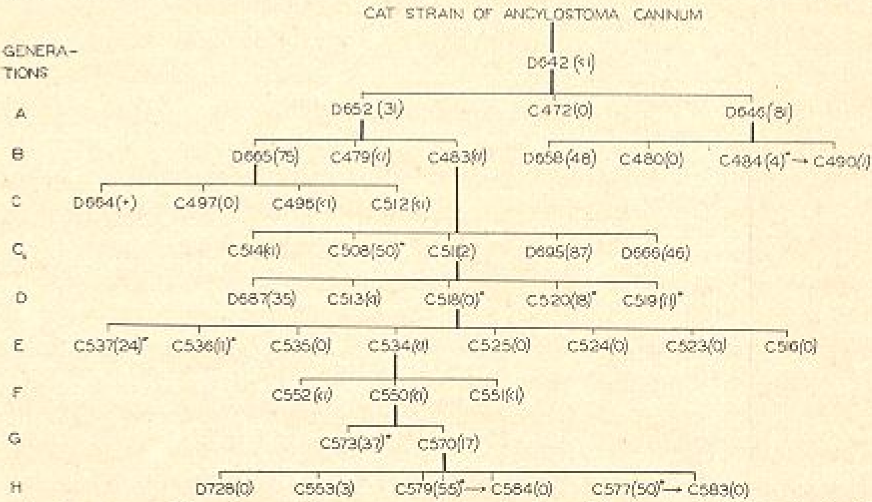

CHART 1. Experimental host passages, beginning with the straight cat strain of *A. caninum.* After the number of each animal is given the percentage development of hookworms based upon the number recovered at autopsy. Stars following these percentages indicate instances where the figures are usually high or low as a result of factors which are explained in the text or in Table 1.

infestations after prepatent periods of 14 and 15 days, respectively, and at autopsy, four weeks after infection, it was found that 48 and 75 per cent of the larvae given had matured. Of the 4 cats, one remained negative 25 days and no worms were found at autopsy. Two others, C 479 and C 483, showed developments of 0.09 and 0.53 per cent. The fourth cat died on the 7th day after infection, and about 700 young worms were recovered from the intestine. Although this represented 3.5 per cent of the number of larvae given (20,000), this figure cannot be regarded as a measure of the infectivity of this strain, since the worms had not matured. The young worms were transferred by gelatin capsule to an uninfected cat (C 490) which, at autopsy 17 days later, yielded 10 worms (1.43 per cent development of the transferred larvae). On the basis of the original larval dose given to C 484, the percentage development to the 24th day in the "secondary" host was about 0.05 per cent. It has been our experience, as it was Scott's (1930, p. 157), that attempts to establish infestations by transferring "half-grown" worms are usually unsuccessful. For this reason, we attach some interest to the above result.

In Table 1, C, are given the data upon the infectivity of the cat strain after one additional generation in dogs. Of this series D 664 had a considerable infestation as shown by a high egg count although the percentage development was not known since the animal was not autopsied. It is quite clear that the infectivity during this and the previous generation was essentially similar to that of the straight dog strain.

In Table 1, C_1, are given the data on a strain which is exactly comparable with that of Table 1, C, except for the last host passage. For this generation the strain was continued through a cat (C 483) after 2 host passages in dogs (see Table 1, B). The behavior of the strain in this generation was looked upon as very important because this originally cat-infective strain had reversed its infectivity after one generation in the dog host, while, on the other hand, it had been observed that the dog strain did not become more infective to cats for at least 3 generations. As far as could be determined from the data, the cat strain had reverted to the dog strain type during the period of our experimental observations. The data have not been easy to interpret. In the first place 3 of the 5 animals were apparently killed by doses of less than 2,000 larvae. Among these animals were the two dogs (D 666, D 695) and one cat (C 508), and their percentages of development are probably exaggerated because, except for D 666 the worms had not yet reached sexual maturity at the time of autopsy. The findings on the other two cats have influenced strongly our interpretation of the findings upon this generation. When both were autopsied, 54 days after infection, it was found that in these hosts, 0.5 and 1.8 per cent of the larvae given had matured. These figures approximate what would have been anticipated had larvae of the straight dog strain been given. Therefore, it is not clear that the infectivity for dogs had diminished nor that the infectivity for cats had increased as a result of the last passage through the cat.

To test the infectivity of the cat strain after two generations in dogs and two in cats (D 642–D 652–C 483–C 511), larvae were cultured from C 511 and administered to 4 cats and 1 dog (Table 1, D). In this instance varying numbers of larvae, in smaller doses, were given and, in addition, the 4 cats were starved for intervals of 14 to 18 days in an attempt to introduce a factor which might (possibly) render them more susceptible to infection. All 5 animals developed infestations, as was determined either by Lane examinations or by recovery of worms at autopsy. Cat 518 showed a prepatent period of 28 days (as did C 519 also) but was not autopsied until the 156th day since it was used as a source of culture to infect subsequent generations. At autopsy, however, no worms were recovered, a result which indicates a short-lived infestation and a consequent inadaptibility between host and parasite. One cat and the dog (C 519 and D 687) were autopsied on the 40th day and yielded developments respectively of 12 per cent and 35 per cent. Cat 520, which had been autopsied still earlier (19 days) showed a development of 18 per cent. It is thus apparent that in comparing the infectivity of these strains, the age of the infestation at the time of autopsy is a factor, since these data and other contained in this report, indicate that in partially refractory hosts the infestations are lost quite rapidly. The development in D 687 (35 per cent), although somewhat lower than the *average* for the straight dog strain, must be accepted as within the range of infectivity. On the other hand, the developments in C 519 and C 520 were significantly higher than has been obtained with the straight dog strain in cats, although these figures have been approached when the cat hosts have been maintained on a deficient diet (Foster and Cort, 1932). It must be concluded that these two cats were abnormally susceptible either as a result of the influence of starvation upon their resistance or in consequence of a favorable change in the infectivity of the strain as a result of the last generation in the cat host. The data of the next generation indicate that starvation was probably the influential factor, even though the starved animals did not become uniformly less resistant.

The strain was continued from C 518 into 8 cats (Table 1, E). One cat died on the 10th day (C 537) and another on the 19th (C 536), although the causes of death are not clear. In these cases all of the worms were still immature, and as has been indicated from previous experiments there were *relatively* large numbers of worms present at autopsy. These, however, as in the earlier cases, cannot be accepted as criteria of the infectivity of the strain. This is further borne out by the fact that on the 21st day 4 additional cats, two of which, in this case also, had been starved, were all negative at autopsy. These findings emphasize again the loss of infestation which takes place in the refractory host just before the parasites reach sexual maturity. Of the two remaining cats, one (C 534) began passing eggs on the 23rd day and was kept as a culture source for the next generation. The other (C 535) was positive to Lane examination on the 25th day, but failed to produce more than

4,000 E. P. D.[1] and soon went negative again. At autopsy no worms were found, an observation which again indicates a short patency in the refractory host. Cat 534 was autopsied on the 82nd day and 8 worms were recovered, representing a development of 0.8 per cent.

From C 534, the strain was continued into the next generation which consisted of 3 cats (Table 1, F). These all began passing eggs on the 24th day, and soon reached egg outputs of from 17,000 to 36,000 E. P. D. Two were autopsied four weeks after infection and showed developments of 0.4 and 0.8 per cent respectively. The other (C 550) was maintained for 165 days and continued to produce about 15,000 E. P. D. At autopsy only 5 worms were recovered (0.07 per cent devel.), which may indicate that part of the infestation had been lost.

Meanwhile, two cats were given larvae cultured from eggs passed by C 550 (Table 1, G). Cat 573 of this generation was given 1,720 larvae and began passing eggs 26 days after infection. Three days later it died, apparently as a result of parasitism, as it was very anemic and 638 worms were recovered. This was equivalent to a 37 per cent development. The other cat (C 570) began passing eggs on the 34th day and reached a maximum of 381,000 E. P. D. on the 66th day after infection. It was not autopsied until the 121st day when 337 worms were recovered. In this case a dose of 2,020 larvae had been given, with the result that the development, after 87 days of patency, was about 17 per cent. In this generation, although the prepatent periods were relatively long and not at all uniform, there was an unexpected degree of infectivity in the cat host.[2]

In view of this result it seemed especially important to observe the infectivity of this strain in an additional generation of cats, and even more important to test again its infectivity for dogs. Therefore, three cats and one dog were given larvae from C 570 (Table 1, H). One cat (C 553) was given an especially large dose of larvae (77,000) and died 12 days after infection, at which time about 2,600 (3.4 per cent development) young worms were recovered from the intestine. The other two cats had been given only 2,000 larvae each, but died on the 27th and 28th days after infection, without having become positive to Lane examina-

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[1] E.P.D. = Eggs per day.

[2] It is desired to acknowledge that this result, inasmuch as it pertains to the 6th generation in cats, contradicts the last sentence of a footnote by Foster and Daengsvang (1932, p. 246) which referred to this work when it was in progress. At that time the autopsy results of this generation were not known, although the behavior during the 5 previous generations and the long prepatent periods in the sixth, seemed at that time, to justify the statement that this strain had apparently not increased in infectivity for cats during six generations in that host. In the light of the data presented at this time, it may be seen that the earlier conclusion was incorrect, since, by autopsy findings, there was apparently an increased infectivity for the cat manifested for the first time in the sixth generation.

tions. From C 577 were recovered 998 worms (50 per cent) and from C 579, 1,100 (55 per cent). Meanwhile the one dog included in this generation had not yet begun passing eggs, with the result that any continued study of this strain appeared to depend upon the successful transfer of worms from C 577 and C 579 to uninfected cats. Therefore, 100 worms from each host were administered by gelatine capsule to C 583 and C 584. Then on the 32nd day, D 723 was autopsied but no worms were found. It is unfortunate that the importance of testing this strain in more dogs had not been foreseen, and especially so, in view of the fact that the worm-transfers to C 583 and C 584 (autopsied shortly afterwards) failed to establish infestations. Consequently, after having passed the cat strain through two generations in dogs followed by six successive generations in cats, it was impossible to continue the experiments further. It is clear, however, that the findings of this last generation confirmed the recently increased infectivity of this strain for the cat host, and, because of the negative result on one dog, there was an indication of reduced infectivity for the dog host. That this strain produced fatal infestations in cats from doses of only 2,000 larvae is strong evidence of its increased ability to develop in that host. Yet, since the worms did not reach sexual maturity at the time of autopsy, it is probable that the apparent infectivity of this strain is exaggerated in the figures given upon percentage development (Table 1, H). Moreover, the extended prepatent periods (over 27 days) suggest a doubt that this strain had yet reached the condition of adaptability to the cat which is exhibited by the straight cat strain.

DISCUSSION

The available evidence seems to indicate that the cat strain is the less stable or the "weaker" of the two strains. It is less widely distributed in nature (Scott, 1929) and as a rule cats are not so frequently infected nor are their infestations as large as in dogs. It has an inherently lower infectivity for the cat host than has the dog strain for the dog (refs. cit.), and also a lower viability of eggs and larvae (Foster and Daengsvang, 1932). The cat strain also develops less well in dogs than does the dog strain in cats. Moreover, it exhibits in the normal host a slower growth rate and reaches a smaller adult size (Scott, 1929 b, 1929 c) and has a lower average egg production per female worm (McCoy, 1931). Growth and egg output, however, do not appear to be inherently controlled functions of the worms but seem rather to be regulated by the host. When infestations of the cat strain were established in dogs, Scott noted that the worms matured as rapidly and reached as large a final size as did worms of the dog strain in this host. The egg production per female worm was found by McCoy to be about the same for both strains in the cat (about 2,400 E. P. D.) and this figure was multiplied several times in the case of infestations of either strain in the dog host.

The present findings confirm Scott's (1930) observation that the infectivity of the cat strain is reversed after a single passage through the dog host. Moreover, it seemed in the present study, that once this change had taken place, the strain behaved like the dog strain, retaining its infectivity for the dog during several successive generations in cats. After the fifth generation, however, the strain appeared to be regaining its infectivity for cats, although the data are insufficient to establish definitely this apparent evolution of strains.

These results point also to a deficiency in our knowledge of the stability of the straight dog strain, since the effect upon this strain of as many as seven successive generations in cat hosts has not been determined. It does not appear, however, that there is anything in our present findings to contradict the view that the dog strain is older biologically and perhaps ancestral to the cat strain. This view, in turn seems to suggest that the evolution and experimental behavior of these strains might be explained by simple biological selection. The difficulty with this hypothesis, however, is that it lacks adequate experimental testing and is not easily harmonized with certain experimental findings, such, for example, as the increased development of these parasites in starved hosts or those on deficient diets. Also in experimental infections of susceptible normal hosts some of the larvae which fail to develop are found to be viable and infective to other susceptible hosts.

Besides having suggested experimentally an apparent evolution of these strains, this study has thrown some additional light upon the biology of the dog hookworm. It has been indicated, for example, that starvation may render a refractory host less resistant to parasitism, an effect which is comparable to that of a deficient diet (Foster and Cort, 1932). Also the behavior of *A. caninum* in partially abnormal hosts has been observed with interest because of its possible bearing upon the mechanism or operation of host resistance. The refractory condition manifests itself in a longer prepatent period, shorter patent period, decreased egg output of the infestation, and in a lower percentage development. Moreover, in the partially refractory host a significant proportion of the infestation is eliminated just before the worms reach sexual maturity. It seems possible that this phenomenon may be associated with the difficulty of establishing infestations by the transfer of "half-grown" worms. This is perhaps an indication that the infective larvae have a greater facility of orientation than have worms whose development is already initiated.

A. caninum is a common parasite of cats and dogs throughout the temperate and tropical world, and the relationships between the strains normally infecting these hosts seem to be as discussed above. This parasite has occurred, however, in many other hosts such as the jackal, wolf, fox, yagouroundi, tiger, sloth-bear, and raccoon. One of the present authors (A. O. F.) has identified *A. caninum* from the Central American puma[3] (*Felis bangsi costaricensis* Merriam) which appears to be an unrecorded host for this species. He was also fortunate to have observed two interesting hookworm infestations in four-week-old Panama yagouroundis (*Herpailurus yagouroundi panamensis* (Allen)). These were litter mates which died after a short period in captivity although they ate well and should have thrived. At autopsy mixed infestations of *A. caninum* and *A. pluridentatum* were found. One harbored 17 specimens of the former and 59 of the latter species, while the other yielded 15 and 94 specimens respectively. The deaths were attributed to hookworm infestation. This shows that *A. caninum* may occur naturally in many wild relatives of cats and dogs and that in some of the observed cases the infestations have been large enough to suggest that they may be, perhaps, something more than examples of accidental parasitism. It would be of interest to test the infectivity of some of these wild strains in cats and dogs, for comparison with the two physiological strains which are especially adapted to these hosts.

ABSTRACT SUMMARY

Continuing an experimental inquiry into the stability of the two physiological strains of *Ancylostoma caninum* which was begun by Scott in 1929, data were obtained upon the behavior of the cat strain during two generations in dogs followed by seven successive generations in cats. Scott's observation that the cat strain took on the infectivity of the dog strain after passage through the dog host was confirmed. It was found further that, when this change had occurred, the strain remained highly infective to dogs and only slightly so to cats for several successive generations in cat hosts. From the fifth to the seventh generations, however, the strain seemed to regain in part its infectivity for cats. It was thought that this might constitute an experimental evolution of these strains, and it was concluded that the dog strain was more stable than the cat strain and probably ancestral to it.

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