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Effects of bot fly (*Alouattamyia baeri*) parasitism on a free-ranging howler monkey (*Alouatta palliata*) population in Panama

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(With 1 plate and 7 figures in the text)

To evaluate effects of persistent bot fly (*Alouattamyia baeri*) parasitism on a host population of Panamanian howler monkeys (*Alouatta palliata*), a 68-month study was carried out which included: (i) examination of the parasite's life cycle; (ii) monthly estimates of prevalence and mean intensity; (iii) monitoring of howler mortality; (iv) censuses of howler monkey troops; and (v) analysis of blood samples from infected and uninfected monkeys. A complete life cycle of *A. baeri* takes approximately 13 weeks; larvae remain in howlers for approximately six weeks, passing through three instars. Overall prevalence of infection was 60%, overall mean intensity 2.8 ± 0.04. No difference in prevalence or mean intensity was found between adult males and females. As a class, juveniles had a significantly higher prevalence and a significantly lower mean intensity than adults; the adult and juvenile classes both showed a significantly higher prevalence and mean intensity than the infant class. Such differences may relate to characteristics of younger age classes rather than host selectivity on the part of the parasite. Although larvae were observed in the howler population throughout the year, relative density fluctuated from month to month, showing from one to three significant peaks per year. Larvae were most abundant during the mid-to-late rainy season (Aug.–Nov.). Relative density was strongly correlated with howler mortality. Several hematological parameters including serum albumin levels and albumin/globulin ratio were significantly lower in individuals with heavy larval burdens. No endoparasites or diseases were found in blood samples. I conclude that the annual pattern of howler mortality results from a synergistic effect between the age, physical condition, and fat reserves of parasitized individuals, the size of the larval burden, and increasing dietary stress as the rainy season progresses. The lack of growth in this closed primate population over >20 years apparently results, in large part, from primary and secondary effects of bot fly parasitism.

Introduction

Ample evidence supports the view that parasites are important in the biogeography and ecology of many animal species (Anderson & May, 1979, 1982; May & Anderson, 1979, 1983; Holmes, 1983; May, 1985, 1991; van Riper *et al.*, 1986). A number of theoretical models and some studies have addressed the role played by parasites in the survivorship or other demographic parameters of a wide range of host populations, including humans (May & Anderson, 1979; Crompton & Nesheim, 1982; May, 1985; Toft & Karter, 1990; Washburn, Mercer & Anderson, 1991; Bergstrom, 1992). The virulent effects of some parasites, particularly viruses and bacteria, are well appreciated (Fenner & Ratcliffe, 1965; May & Anderson, 1983; Harwood & Hall, 1990); considerable data also indicate that many other parasites (e.g. nematodes, helminths, ticks) may impact negatively on hosts (Holmes, 1983; Crompton *et al.*, 1985; van Riper *et al.*, 1986; Jaenike 1988; Keymer & Read, 1991; Hudson, Dobson & Newborn, 1992; Herre, 1993).

Traditionally, 'successful' parasites tend to be viewed as commensal or 'well adapted' to their hosts (prudent parasite model, Holmes, 1983) and thus unlikely to produce harmful effects (Catts, 1982; May & Anderson, 1983; Toft & Karter, 1990; Munger & Karasov, 1991). Such benign relationships might be expected to be particularly obvious in obligate parasites, dependent on particular host species for one or more life stages. Some evidence to refute this traditional view has recently been presented which shows that, at times, even highly host-specific parasites may affect hosts adversely, causing injury or death or lowering growth or reproductive output (e.g. Schall, 1983*a*, *b*; Jaenike, 1988; Keymer & Read, 1991; Herre, 1993; Ebert, 1994). Furthermore, there is little evidence to suggest that hosts are ever passive in the face of parasitic infestation and considerable evidence to suggest that they are not (Payne *et al.*, 1965; Jacobson, McGinnes & Catts, 1978; Timm & Cook, 1979; Schall, 1983*a*, *b*). The massive damages reported for some mammalian species inadvertently parasitized by parasites specific to another host species (e.g. Wecker, 1962; Smith, D. H., 1977; Jacobson *et al.*, 1978; Guimaraes & Coimbra, 1982) suggest that some degree of tolerance to the parasite by the correct host may have evolved (or be induced), but it also suggests that the costs of such tolerance may be high.

To evaluate the demographic or other effects of a host-specific parasite on its host, I carried out a study of the howler monkey bot fly (*Alouattamyia baeri*), focusing on its interactions with a closed population of mantled howler monkeys (*Alouatta palliata*) in Panama. Anderson & Gordon (1982) have stressed the technical difficulties inherent in establishing 'clear evidence' of parasite-induced host mortality in the natural environment. Results of this study, though largely correlational, suggest that bot fly larvae contribute to howler mortality each year, affecting immature monkeys most heavily. The lack of growth in this wild monkey population over a period of >20 years apparently results, in large part, from primary and secondary effects of bot fly parasitism.

Methods

Study site

Field observations and larval collections were made on Barro Colorado Island (BCI), a 15.5 km^2 nature reserve in the Republic of Panama. Detailed descriptions of the island and its flora and fauna can be found in the literature (e.g. Leigh, Rand & Windsor, 1982; Hubbell & Foster, 1990). Climatic conditions in this region are characterized by a rainy season lasting some seven months (May–November), followed by a 4–6 week transition season (mid-December–mid-January) and then a 3 month (mid-January–mid-April) dry season (Fig. 1). Climatic features such as temperature and rainfall have been suggested to affect bot fly abundance at some locales (Mourier & Banegas, 1970; Brigada, Tripole & Zuleta, 1992; Bergstrom, 1992; Vieira, 1993). On BCI, daily climatic information on a number of features is routinely compiled and made available to researchers.

Parasite and host

Cuterebrid bot flies comprise a specialized line of myiasis-producing primitive calypterates confined to the New World (Catts, 1982). Little is known about their biology and life history, particularly in tropical regions (Vieira, 1993). To date, the best studied cuterebrid is *Dermatobia hominis*, sometimes, though incorrectly, referred to as the human bot fly. This monospecific genus lays its eggs primarily on mosquitoes and muscoids (Zeledón, 1957; Catts, 1982). When the carrier insect visits a vertebrate host to feed, larvae emerge from eggs and penetrate the host's skin where they pass through 3 instars as subcutaneous parasites. The wide range of hosts tolerated by *D. hominis* strongly contrasts with the behaviour of other cuterebrid species which typically are obligate larval parasites of specific host species and whose larvae enter and pass much of

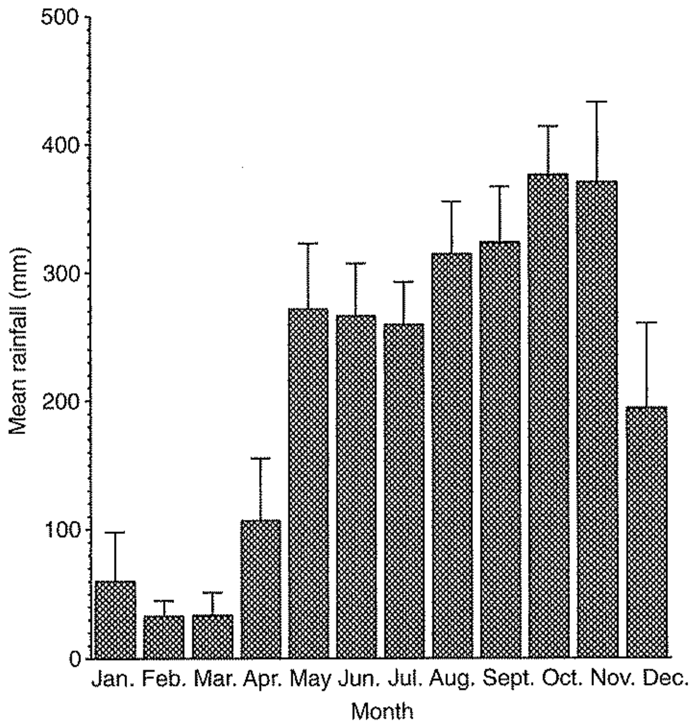

FIG. 1. Average (± S.E.) monthly rainfall in mm for Barro Colorado Island between 1973–1993. Based on 20 years of daily rainfall collection compiled by the Environmental Sciences Program, Smithsonian Institution.

the first instar within the body system of the host, that is internally not subcutaneously (Smith, D. H., 1977; Jacobson *et al.*, 1978; Catts, 1982). Larvae migrate internally, typically to a specific site on the host's body, open larval pores and pass through 2 more instars before dropping to the ground to pupate (Catts, 1982).

The bot fly, *Alouattamyia baeri*, was first described by Shannon & Greene (1926). As the name implies, this species is closely associated with the genus, *Alouatta*, or howler monkey, a primate with a wide geographical distribution extending from southern Mexico to northern Argentina (Milton, 1980, 1993). Howler monkeys are arboreal primates, weighing 6–8 kg as adults. Their diet consists of a wide variety of new leaves, fruits, and flowers (Glander, 1978; Milton, 1980). Six species of *Alouatta* are recognized. Undoubtedly, *A. baeri* larvae are usually specific to members of the genus *Alouatta*. On BCI, where there are 5 non-human primate species, *A. baeri* larvae have been observed only in association with *A. palliata*. Goldmann (1920), who collected *A. palliata* specimens in mainland forest near BCI some 75 years ago, noted that *A. baeri* larvae were numerous in the howler monkeys he collected but were not found on any spider monkeys (*Ateles* sp.) at the same site. With few exceptions (one involving a night monkey, *Aotus* sp. (Guimaraes, 1971) and several involving human hosts (Guimaeres & Coimbra, 1982; Fraiha *et al.*, 1984)), *A. baeri* larvae have been reported only in association with howler monkeys [e.g. Costa Rica (Zeledón, Jiménez & Brenes, 1957); Panama (Shannon & Greene, 1926; Dunn, 1934), Guyana (Shannon & Greene, 1926), Brazil (Shannon & Greene, 1926; Guimaraes, 1971) and Venezuela (M. Lizarralde, pers. comm.)].

Because Barro Colorado is an island, the howler monkey population is closed to emigration or immigration. Changes in its size can therefore come about only through births or deaths (Milton, 1982). Howler monkeys in mainland forests adjacent to BCI likewise host larvae of *A. baeri*.

Although howler monkeys actively repel flying insects (Dudley & Milton, 1990), unlike other New World monkeys, they typically do not auto- or allogroom, a trait which might suggest increased susceptibility to ectoparasites. However, first instar bot fly larvae are minute and, once hatched, rapidly enter a potential host's system (D. Colwell, pers. comm.). Once the larval pore is opened, larvae are firmly fixed so that even humans, with their high degree of manual dexterity, and strength must use tremendous force to expel them. I predict that no monkey species would be able to perform this action. The association of a host-specific bot fly with howler monkeys is presumably related more to distributional, physiological, or behavioural characteristics of the genus *Alouatta* than to benefits conferred by grooming.

General data collection

Data collection was begun in May 1986; materials presented here cover observations through December 1993. Life history data on the parasite were obtained by observations of *A. baeri* larvae in howler monkeys, as well as the study of larvae removed from monkeys captured with tranquillizing darts. All captured monkeys were given a physical examination, sexed, and weighed; larvae were counted and instar stages and locations recorded. In August 1991 and 1992, live larvae were collected for study; 3 larval warbles were excised to document size and thickness. In both 1991 and 1992, blood samples were collected from captured monkeys. Complete blood counts (CBCs) and serum chemistry panels (CHEM20) were performed on samples to examine effects of *A. baeri* larvae on hosts (i.e. evidence of infection, haematological abnormalities) and check for evidence of other parasites, pathogens or diseases. Sera from infected and uninfected howler monkeys were tested for the presence of anti-*Alouattamyia* antibodies to first and third instar antigens using an ELISA. Faecal samples were collected in 1991 and 1992 to analyse for intestinal parasites. In 1991, sterile swabs of 12 third instar larval capsules were taken to determine the presence of bacteria or infection. Some results of this clinical work are presented here; detailed results will be presented elsewhere (Milton *et al.*, In prep.; Baron, Colwell & Milton, In prep.).

Larval body composition

To help evaluate costs to hosts of rearing bot fly larvae, analyses of 2 late third instar larvae were carried out to determine their content of lipid, protein, and nonstructural carbohydrates. All tests were done in replicate on dried material. Lipids were estimated by the chloroform extractant technique; nitrogen was determined by the micro-Kjeldahl technique with the 6.25 conversion factor used to estimate crude protein; non-structural carbohydrates were estimated by the modified Weinman technique (Smith, 1969).

Samples of larval infestation

In January 1987, a sampling program was begun to examine the pattern of bot fly parasitism in the BCI howler population. In each sample, using binoculars, all visible bot fly lesions on each monkey were counted and their locations recorded; bot fly lesions are large and conspicuous and can typically be seen even without binoculars (Plate I). The number of monkeys examined in each month of data collection are presented in Table I.

As shown in Table I, initially, between 50 and 100 monkeys were examined twice per year, but in July 1988, monthly data collection was begun and in March 1989, to achieve a more balanced research design, monthly sample size was set at 80 monkeys, composed of 20 individuals from each of 4 age classes (adult

PLATE I. Adult male howler monkey with three late-third instar and two early-third instar larvae of *Alouattamyia baeri*, the howler monkey bot fly.

male, ≥5 yrs of age; adult female, ≥5 yrs of age; juvenile, >12, <60 months of age; infant, >0, ≤12 months of age). In most years, immature monkeys were further characterized by stage of development (i.e. infant 1 (0–2 months), infant 2 (>2, 6 months) and infant 3 (>6–12 months) and juvenile 1 (>12–24 months), juvenile 2 (>24–36 months) and juvenile 3 (>36, <60 months). To avoid observer bias, monkeys were examined according to a set protocol based on the order in which individuals were first sighted. To ensure that samples represented infestation rates from a range of different troops, no more than 8 individuals, 2 from each age class, could be examined per troop per month. There are approximately 60 howler troops on BCI, providing a substantial sample pool. In any given monthly sample, the *a priori* assumption was that any

TABLE I

Number of monkeys sampled for bot fly larvae in each of 68 sample months

	Month											
Year	Jan. N	Feb. N	Mar. N	Apr. N	May N	Jun. N	Jul. N	Aug. N	Sept. N	Oct. N	Nov. N	Dec. N
1987	70	–	–	–	–	–	–	–	–	–	–	98
1988	55	–	–	–	–	–	91	102	106	97	103	106
1989	85	81	80	80	80	80	80	80	80	80	80	51
1990	–	83	80	80	80	80	80	81	80	80	80	80
1991	80	80	80	78	80	80	80	81	80	80	80	80
1992	80	80	80	80	80	80	80	71	80	75	79	77
1993	77	77	77	78	79	79	79	80	80	80	80	80

troop or monkey on the island had as good a chance of being examined as any other troop or monkey, and that no troop or monkey would be examined more than once. Samples generally were taken within the same 7–10 day period each month.

Troop censuses

Censuses to monitor the howler population for changes in troop size or composition were first begun in 1977 (see Milton, 1982 for earlier censusing results). Troops were selected by chance encounter while walking the BCI trail system. Once a troop was located, each monkey was examined with binoculars and its approximate age and sex (if adult) was noted; immature howlers cannot be sexed using binoculars but can be assigned to one of the developmental stages described above. For this study, the same sampling protocol was continued over the period 1986–1993.

For analytical purposes, data from any month between Jan. 1977 and Dec. 1993 in which $\geqslant 5$ troops were counted were used to estimate mean troop size and composition for that month. A total of 31 months representing 16 years between 1977–1993 qualified for analysis (i.e. had $\geqslant 5$ troops sampled in that month). Sample size generally ranged between 8 and 10 troops censused per month. Seven years between 1977–1993 had only a single census month while one year, 1988, had six. An island-wide census in 1988 gave a total estimate of 60 howler troops, approximately the same number as found in 1977 and 1979 (Milton, 1982). Thus, a total of 60 troops was consistently used with monthly means of troop size to estimate island-wide population size.

Mortality data

Earlier work (1977–1979) had shown a persistent annual mortality peak in howlers during the mid-to-late rainy season, August through November (Milton, 1982). To document this pattern better as well as seek factors related to it, in July 1986, a program was begun to collect information on howler mortality on BCI. To ensure that cadavers would be reported, a bounty was paid for each howler monkey skull turned in to the sampling program. With the skull, the age and, if adult, sex of each cadaver could also be determined. Each person finding a cadaver filled out a data sheet giving the date and place of the encounter, the condition of the cadaver, and the finder's habitual pattern of activities in the forest. My evaluation of the accuracy of this collection program is presented in the **Results**. Very occasionally, cadavers were recovered while still fresh enough for autopsy. In such cases, the body was taken to a veterinary clinic on a US military base in Balboa, Panama for examination.

Other than damages from bot fly larvae, seasonal low points in the availability of higher quality plant foods had been suggested as one possible factor contributing to the annual rise in howler mortality each rainy season (Milton, 1982). Due to a high digestible energy content relative to foliage, ripe fruits are regarded as high quality plant foods (Milton, 1979, 1980). Each year, there are 2 fruiting peaks by canopy trees on BCI, a broad strong peak in the early rainy season May–June, followed by a brief trough (July) and then a second narrow peak in Aug.–Sept. (Foster, 1982*a*, *b*). However, fruits (and new leaves) of *Ficus* spp., the single most important food genus for howler monkeys on BCI, do not conform to this pattern. Foods from this genus are far more abundant during the drier 6-month portion of the year (Dec.–May) and generally are in short supply during the late rainy season (October–mid-December; Milton, 1991). On BCI, annual patterns of fruit production have been monitored since 1987 by a sampling program in which, each week, all fruits falling into 200 identical fruit traps are removed, counted, and identified as to species (O. Calderon & S. J. Wright, work in progress). These data enabled me to compare annual fruit production patterns with my data on howler mortality.

Predation has been suggested to affect the size of some primate populations (Terborgh & Janson, 1986). However, in more than 64 years of observation, there is only one report of attempted predation on a howler on BCI, in this case, an unsuccessful attack by an ocelot on a juvenile monkey (Carpenter, 1934). Though ocelots (and occasionally jaguars) still occur on BCI, vertebrate predation on howler monkeys at this site appears to be extremely rare and, in my view, should produce no detectable change in any population parameter (see also Carpenter, 1934).

Definition of terms and data analysis

Following Margolis *et al.* (1982), *prevalence* refers to the number of infected monkeys in any given sample divided by total sample size. *Mean intensity* refers to the number of parasites counted in any given sample divided by the number of infected monkeys in that sample, and *relative density* to the number of parasites counted in any given sample divided by the total number of monkeys, infected plus uninfected, in that sample. Relative density thus equals prevalence times mean intensity.

Statistical analyses were carried out using the Statistical Analysis System (SAS) package, release 6.09. Correlation coefficients were computed using the SAS procedure CORR. Prevalence, mean intensity, and relative density were examined using the SAS procedure NPAR1WAY; when data for the variable had 2 levels (e.g. male, female), the Mann–Whitney U-test was used; when data had 3 or more levels (e.g. adults, juveniles, infants), the Kruskal–Wallis test was used. For these and all other tests, differences were considered to be significant at levels of $P \leqslant 0.05$. To test whether months or years differed significantly from each other in terms of larval parameters, an ANOVA was used to perform Tukey's studentized range test (HSD).

To test for the presence of peaks in larval density, Duncan's multiple range test was used. For this test, a peak was defined as a period of one or more concurrent months having a higher mean bot infestation rate than adjacent months, and also differing significantly from those months. Duncan's test was performed on each year separately, with each year also including the preceding December and the subsequent January to discern January and December peaks. Thus, each full year possessed 14 separate means from which to discern peaks. To test for periodicity in monthly data on relative density, spectral analysis was carried out using the statistical package SPSS.

The dispersion pattern of larvae among hosts over the total sample was assessed by calculating the index of dispersion (ID) as $\mathrm{ID} = s^2/m$ where m is the mean number of parasites per host and s^2 is the variance. If ID is >1.0, this indicates a clumped or aggregated pattern of parasites among hosts. The frequency distribution of larvae was then compared with an expected distribution generated by a Poisson according to the equation $\mathrm{P(n)} = (\mu \mathrm{n\,e}-\mu)/\mathrm{n}!$ (Sokal & Rohlf, 1973) where $n =$ the number of bot fly larvae per sample individual and $\mu =$ the mean number of bot fly larvae per sample individual. The number of larvae per sample individual (=larval distribution) was defined from $0 =$ no larvae present on a sample individual to $\geqslant 7$ larvae present on a sample individual. Results were then tested for significance with a χ^2 test for difference between the observed and expected distributions.

Results

Description and life cycle of the parasite

First, second, and early third instar larvae of *A. baeri* are cream in colour. Maturing third instar larvae darken from pale red to black and are heavily corrugated. Third instar larvae approaching the pupation stage are about 2.4 cm in length and 1.5 cm in width with an average weight of 2.5 g (S.D. $\pm$ 0.38 g, $n = 17$); some larvae weigh > 3 g. Larval body composition ranged between 17 and 23% lipids, 47 and 48% protein, and 6 and 7% non-structural carbohydrates.

Adult *A. baeri* are large (18 to $\geqslant 20$ mm in length) black flies. The dorsal portion of the body and legs are covered with a dense coat of short, velvety black hairs, while the wings are transparent amber-brown. Adults produce a buzzing sound in fast flight; both in appearance and sound, they suggest large neotropical bees—a possible convergence feature that may afford flies some protection from predators. Flies hatched from larvae removed from howler monkeys on BCI are stored as reference specimens in the laboratory of KM at Berkeley.

The oviposition site of *A. baeri* is unknown. Similar to most cuterebrids, adult flies are hypothesized to deposit eggs on foliage or other plant material in locales likely to be visited by howlers (Shannon & Greene, 1926; Catts, 1982). Laboratory studies at Lethbridge Research Station, Alberta, Canada, using flies reared from *A. baeri* larvae collected from howler monkeys on BCI show that females average 1400 eggs; eggs are deposited in rows of from 58 to 165 eggs (D. Colwell, pers. comm.). Not all of the larvae in an egg cluster will emerge synchronously following an appropriate stimulus (i.e. rapid warming and an increase in carbon dioxide concentration); rather, only around 10% of the cluster emerge at any given time (D. Colwell, pers. comm.). This phenomenon has also been noted in other cuterebrids (Catts, 1982). Eggs are 'boat-shaped' (*sensu* Leite & Williams, 1989), black in colour and highly rugose. Once contact with a host is effected, larvae enter the internal system through the nares and mouth and migrate internally to sites in the neck region where they open larval pores. A few larvae may also establish on the face, back, chest or axillary regions of the host. Commonly, howler monkeys host larvae in different instars (Plate I), when the already parasitized monkey has presumably been reinfested by later contact with other larvae.

Larvae remain in howlers slightly less than six weeks, passing through three instars (Fig. 2). Once the third instar is completed, larvae leave the warbles and drop 15 to >25 m to the ground where they burrow into the soil to pupate. An experiment in Panama, using 13 live larvae and 4 cm of soil covered with fallen leaves showed that larvae actively enter the soil and do not simply burrow under leaf litter. Pupal development of two larvae maintained under ambient conditions in Panama took between 41 (male fly) and 48 (female fly) days; the male fly was notably smaller than the female. Both under ambient conditions in Panama and under controlled laboratory conditions (26 °C, 65% relative humidity), adult flies lived only four or five days and, although provided with water and fruit pulp, were not observed to drink or eat. As, on average, a complete life cycle of the howler monkey bot fly on BCI is estimated to take approximately 13 weeks (Fig. 2), three generations of *A. baeri* should be possible each year.

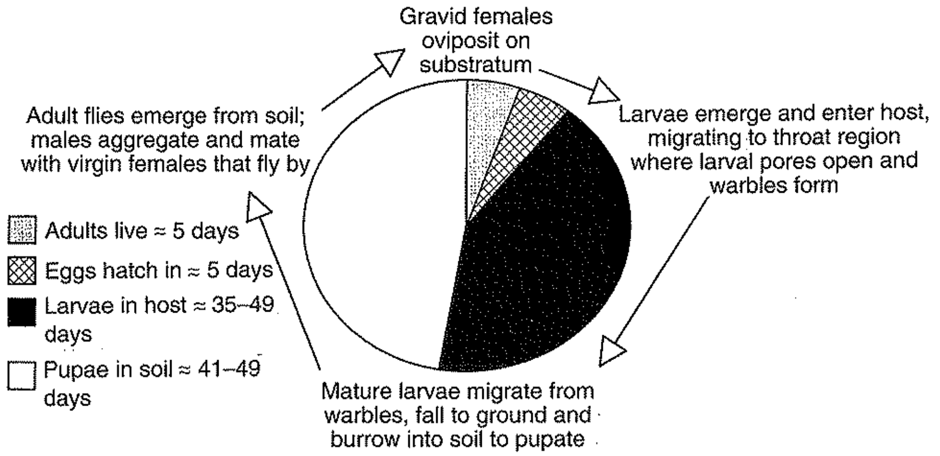

FIG. 2. Proposed life cycle of *Alouattamyia baeri* on Barro Colorado Island, Republic of Panama.

Host response to bot fly larvae

Howler monkeys develop a collagenous capsule (larval warble) to wall off larvae, generally one capsule per larva, though occasionally two larvae are found within the same capsule (see also Wecker, 1962). These capsules are impressive in size with dimensions paralleling those of larvae as described above and with a thickness of 3–5 mm. Monkeys show a strong inflammatory response to the first instar stage; as the larval pore is opened, the host's skin becomes visibly reddened and unusually warm to the touch. Aerobic, bacteriologic culture of swabs taken of third instar botfly capsules revealed secondary contamination with potentially pathogenic bacteria in 11 of 12 samples examined: coagulase-positive *Staphlococcus* was recovered from bot lesions in 6 of 12 animals. Yet capsules containing larvae are not infected indicating that infections may proliferate only after larvae have quitted capsules to pupate.

Tests to determine the presence of anti-*Alouattamyia* antibodies in sera of howler monkeys showed that howlers produce antibodies to both first and third instar larvae as measured by an immunosorbent enzyme-linked assay (ELISA). The response to first instar antigen is directly correlated to infestation levels; however, no correlation was observed for the response to third instar antigen (Baron, Colwell & Milton, In prep.). These antibodies may be implicated in limiting larval bot fly numbers.

Most analyses of howler monkey blood samples ($n = 57$) fell within the reference ranges considered normal for the species (Milton *et al.*, In prep.). However, bivariate regression analysis revealed a significant negative relationship between bot fly larval burden and several haematologic parameters, including total plasma proteins ($r^2 = 0.069$, $F = 5.027$, $P = 0.128$), serum albumin/globulin ratio ($r^2 = 0.410$, $F = 30.62$, $P < 0.0001$), and total serum albumin ($r^2 = 0.435$, $F = 33.87$, $P < 0.0001$). Forty-three percent of the variability observed in serum albumin levels was explained by larval burden. Albumin and globulin comprise the major components of total plasma proteins; the strong negative relationship found for serum albumin levels also accounted for the significant findings for total plasma proteins and the albumin/globulin ratio.

Blood samples showed no evidence of parasites such as microfilaria or plasmodia (e.g. malaria), nor were pathogens or diseases detected. Depending on year, faecal analysis showed that between 55 and 86% of the monkeys sampled harboured one or more species of intestinal parasite but with one exception, cysts of *Giardia lamblia* found in a total of 15 individuals ($n = 34$), the parasite species so identified may be nonpathogenic (J. Theis, pers. comm.). Bot fly larvae removed from howler monkeys showed no evidence of nematodes or other parasites that might secondarily infect the host (G. Poiner, pers. comm.).

Attraction of ***Cochliomyia hominivorax***

Howler monkeys occasionally scratch third instar lesions, drawing blood. Further, after a larva quits the warble capsule, it remains open for several days, typically with a conspicuous fluid discharge. These open wounds may attract the attention of *C. hominivorax*, the primary screwworm fly, whose larvae have been removed from dying howler monkeys on BCI and identified (A. Broce, pers. comm.; N. Gale, pers. comm.). If gravid females of *C. hominivorax* are attracted to *A. baeri* lesions and oviposit, the monkey will die from septicemia or destruction of vital tissues. In three such cases, the screwworm-infested wound appeared to have been acquired in a fight or fall; in three other cases, recently evacuated larval warbles of *A. baeri* appeared to have been the attractant.

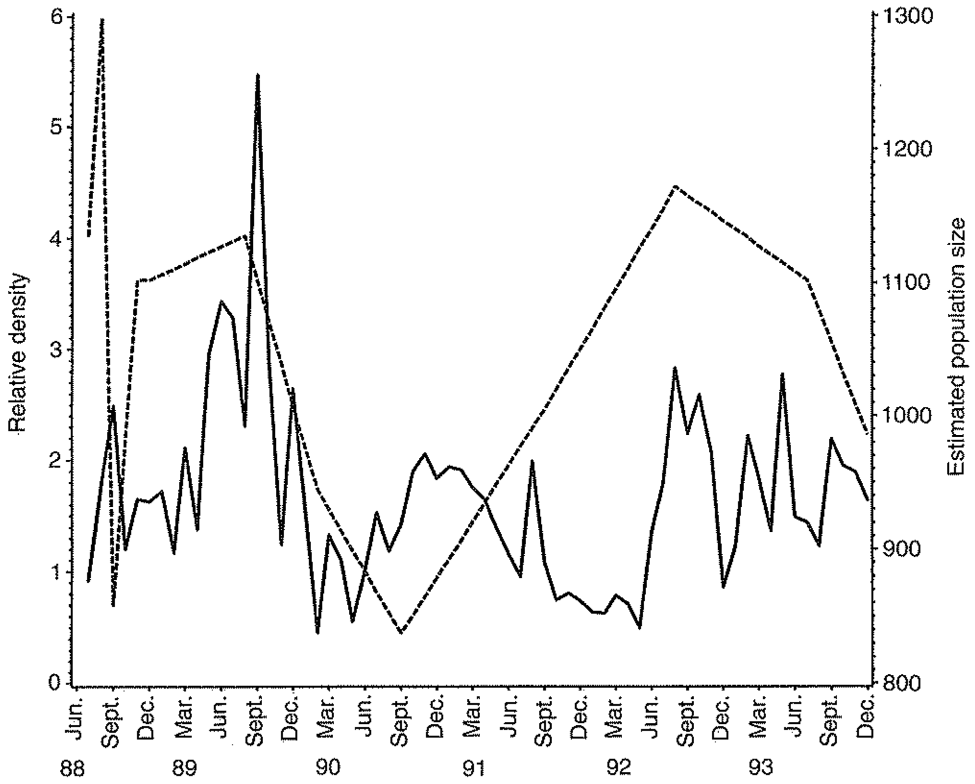

FIG. 3. Relative density of larvae in the howler population in monthly samples July 1988 through December 1993 (solid line; see also Table I) compared with estimates of total population size over the same time period (hatched line). A total of 60 howler monkeys troops was consistently used as the basis for all population estimates.

Annual distribution pattern of larvae

Monthly relative density showed distinctive fluctuations (Fig. 3). Duncan's test showed that each sample year was characterized by one or more significant peaks in relative density. In both 1989 and 1993, three significant peaks per year were found [1989—(a) May through July, (b) Sept., and (c) Dec.; 1993—(a) Feb., (b) May, and (c) Sept.]. Other years showed a single peak (1988—Sept.; 1990—March; 1991—Aug.) or a run of months as a single peak (1992—Aug. through Oct.). Spectral analysis of relative density over the total sample period suggested a cycle of a three-month period, which is consistent with the estimated life cycle of the parasite. On the whole, data suggested that three generations of larvae per year may be the norm—one in the late dry season, another at the beginning of the rainy season, and a third in the mid-to-late rainy season around September.

Some *A. baeri* larvae are always present in the howler population. This suggests either that a certain percentage of adult flies consistently breed and oviposit outside periods related to peaks, or that eggs or pupae of *A. baeri* can persist for some time in the environment, depending on the opportunity to contact howler hosts or environmental conditions. Cuterebrid eggs have a tough chorion which helps to ensure a long period of hatching; further, among some species, the duration of pupal development can vary, depending on temperature or other factors (Dunaway *et al.*, 1967; Smith, D. H., 1977). Factors affecting the timing of bot fly generations each year are as yet unknown, but limited data suggest that rainfall and its effects on other environmental parameters, possibly soil moisture, may be involved.

Dispersion pattern of larvae on hosts

The index of dispersion (ID, variance-to-mean ratio) of bot fly larvae in the howler population was greater than 1 (ID = 3.07), suggesting an aggregated pattern of parasites among hosts. When larval distribution was tested against a Poisson distribution, the difference from expectation was highly significant ($\chi^2 = 7582$, $d.f. = 7$, $P \ll 0.005$), supporting the view that larvae are not randomly distributed among hosts but rather are aggregated, with some hosts receiving a disproportionate share.

Prevalence, mean intensity, relative density

Though these three parameters derive from the same data, each can convey distinct information about the pattern of infection in any particular sample. In this study, changes in these parameters were positively correlated.

Overall prevalence for the total sample was 60% (S.E. ± 0.0007, $n = 5496$). Prevalence differed significantly between sample years (ANOVA, F = 30.32, $d.f. = 6$, $P = 0.0001$). The most

TABLE II

Prevalence, relative density and mean intensity of bot fly larvae in the howler monkey population by year and by month over the total sample period

Year*	No. monkeys	Prevalence (% ± 1 S.E.)	Relative density (x̄ ± 1 S.E.)	No. monkeys	Mean intensity (x̄ ± 1 S.E.)
1987	168	53 ± 0.04	1.0 ± 0.10	89	1.9 ± 0.13
1988	660	55 ± 0.02	1.5 ± 0.09	364	2.8 ± 0.12
1989	937	76 ± 0.01	2.5 ± 0.10	715	3.3 ± 0.11
1990	884	57 ± 0.02	1.3 ± 0.06	505	2.3 ± 0.09
1991	959	59 ± 0.02	1.4 ± 0.06	568	2.3 ± 0.08
1992	942	48 ± 0.02	1.4 ± 0.07	451	2.9 ± 0.11
1993	946	62 ± 0.02	1.8 ± 0.07	590	2.8 ± 0.09
Month**					
Jan.	447	59 ± 0.02	1.3 ± 0.08	263	2.2 ± 0.10
Feb.	401	51 ± 0.02	1.3 ± 0.10	205	2.5 ± 0.15
Mar.	397	56 ± 0.02	1.6 ± 0.11	224	2.8 ± 0.15
Apr.	396	54 ± 0.03	1.3 ± 0.09	215	2.3 ± 0.13
May	399	55 ± 0.02	1.6 ± 0.13	218	3.0 ± 0.19
Jun.	399	57 ± 0.02	1.7 ± 0.12	229	2.9 ± 0.16
Jul.	490	57 ± 0.02	1.6 ± 0.10	281	2.9 ± 0.14
Aug.	495	67 ± 0.02	1.9 ± 0.10	330	2.8 ± 0.12
Sept.	506	69 ± 0.02	2.5 ± 0.14	349	3.6 ± 0.17
Oct.	492	62 ± 0.02	1.8 ± 0.11	307	3.0 ± 0.14
Nov.	502	64 ± 0.02	1.6 ± 0.08	321	2.5 ± 0.10
Dec.	572	59 ± 0.02	1.4 ± 0.07	340	2.3 ± 0.09

* (1987—2 months of data, Jan. & Dec.; 1988—7 months of data, Jan. and July–Dec.; all other years = 12 months of data except 1990 where *n* = 11 months)

** (N = 5 for Feb.–May; N = 6 for all other months except Dec. where N = 7 months) distinctive year was 1989 (Table II); its high prevalence significantly differentiated it from each of the other study years (Tukey's Studentized Range test, $P \leqslant 0.5$ in all cases). In 1989, prevalence was unusually high in all 12 monthly samples, ranging from 57% in February to 91% in July and remaining at 90% in both September and December. In other sample years, though monthly prevalence might reach as high as 72% (Sept. 1993) or 76% (August 1992) or 79% (December 1990), persistent high prevalence similar to that of 1989 was not observed.

When prevalence data for each sample month across sample years were combined (i.e. all data for each January in the study were combined to give a total score for January, all data for each February were combined to give a total score for February, and so on; see Table II), prevalence differed significantly between months (ANOVA, $F = 5.37$, $d.f. = 11$, $P = 0.0001$). September was the single most outstanding month in terms of its high prevalence, differing significantly from six other months (Feb.–July), while August had a significantly higher prevalence than three other months (Feb., April, May) (Tukey's Studentized Range test, $P \leqslant 0.05$ in all cases). To examine seasonal patterns, I divided data into two six-month periods, Jan.–Jun., representing the drier half of the year and Jul.–Dec., representing the wetter half. Prevalence was significantly higher in the wetter period (Tables III & IV).

In combined data, I found no significant difference in prevalence between adult males and adult females (Table III & IV). The juvenile class had a significantly higher prevalence than the adult class; the adult class and the juvenile class each had a significantly higher prevalence than the infant class (Tables III & IV).

Overall intensity averaged 2.8 larvae (S.E. ±0.04, $n = 3282$). Mean intensity differed significantly between sample years (ANOVA, $F = 16.19$, $d.f. = 6$, $P = 0.0001$) and sample months

TABLE III

Prevalence, relative density and mean intensity of bot fly larvae in the howler monkey population by class, by sex (if adult), by stage (if immature) and by half-year periods

Class*	N	Prevalence* (% ± 1 S.E.)	Relative density* ($\bar{x} \pm 1$ S.E.)	N	Mean intensity* ($\bar{x} \pm 1$ S.E.)	Range
Adult male	1320	63 ± 0.01	2.0 ± 0.07	837	3.1 ± 0.09	1–20
Adult female	1512	65 ± 0.01	1.9 ± 0.06	990	3.0 ± 0.07	1–18
Adult (M + F)	2832	65 ± 0.01	1.9 ± 0.05	1827	3.1 ± 0.08	1–20
Juvenile	1316	72 ± 0.01	2.0 ± 0.06	951	2.7 ± 0.07	1–18
Infant	1348	37 ± 0.01	0.7 ± 0.03	504	1.9 ± 0.07	1–10
Immature (J + I)	2664	55 ± 0.01	1.3 ± 0.04	1455	2.4 ± 0.05	1–18
Immature Stages*	N**			N**		
Infant 1	222	13 ± 0.02	0.2 ± 0.03	28	1.3 ± 0.10	1–3
Infant 2	643	40 ± 0.02	0.7 ± 0.05	254	1.7 ± 0.08	1–10
Infant 3	265	64 ± 0.03	1.4 ± 0.10	169	2.2 ± 0.12	1–9
Juvenile 1	301	70 ± 0.03	1.8 ± 0.12	212	2.6 ± 0.13	1–10
Juvenile 2	358	74 ± 0.02	2.0 ± 0.12	266	2.7 ± 0.14	1–18
Juvenile 3	428	81 ± 0.02	2.2 ± 0.11	346	2.7 ± 0.12	1–15
Season						
Lower rainfall (Jan.–June)	2439	56 ± 0.01	1.5 ± 0.04	1354	2.6 ± 0.06	1–20
Higher rainfall (Jul.–Dec.)	3057	63 ± 0.01	1.8 ± 0.04	1928	2.8 ± 0.05	1–18

* As defined in **Methods**

** Stage Ns do not sum to Class N as not all infants or juveniles were classified as to stage in monthly censuses

TABLE IV

Sample size, Z-scores and significance levels for Mann–Whitney U-test comparing half-year periods and different sex-age classes/stages of monkeys in terms of prevalence, mean intensity, and relative density over the total sample period

	N	Z	*P*
Jan.–Jun., Jul.–Dec.			
Prevalence	2439, 3057	−5.6721	0.0001
Mean intensity	1354, 1928	−2.7248	0.0064
Relative density	2439, 3057	−6.2772	0.0001
Adult male, adult female			
Prevalence	1320, 1512	−1.1467	0.2515
Mean intensity	837, 990	−0.3038	0.7613
Relative density	1320, 1512	−1.1369	0.2555
Adults, juveniles			
Prevalence	2832, 1316	4.9398	0.0001
Mean intensity	1827, 951	−3.8346	0.0001
Relative density	2832, 1316	1.9942	0.0461
Adults, infants			
Prevalence	2832, 1348	−16.5022	0.0001
Mean intensity	1827, 504	−11.8739	0.0001
Relative density	2832, 1348	−19.3791	0.0001
Juveniles, infants			
Prevalence	1316, 1348	18.0732	0.0001
Mean intensity	951, 504	−8.1003	0.0001
Relative density	1316, 1348	19.6474	0.0001
Infant 3, juvenile 1			
Prevalence	265, 301	−1.6833	0.0923
Mean intensity	169, 212	−1.5112	0.1307
Relative density	265, 301	−2.2300	0.0257
Juvenile 1, juvenile 3			
Prevalence	301, 428	−3.2632	0.0011
Mean intensity	212, 346	−1.1402	0.2542
Relative density	301, 428	−3.1939	0.0014
Juvenile 2, adults			
Prevalence	358, 2832	3.6733	0.0002
Mean intensity	266, 1827	−2.4947	0.0126
Relative density	358, 2832	1.7069	0.0878
Juvenile 3, adults			
Prevalence	428, 2832	6.6774	0.0001
Mean intensity	346, 1827	−2.4549	0.0141
Relative density	428, 2832	4.1527	0.0001

(ANOVA, F = 8.70, *d.f.* = 11, *P* = 0.0001). The most outstanding year was 1989, which had a significantly higher overall mean intensity than any other sample year (Tukey's Studentized Range test, $P \leqslant 0.05$ in all cases). In combined data, September and May differed significantly from all other months in terms of high intensity (Tukey's Studentized Range test, $P \leqslant 0.05$ in all cases). In combined data, mean intensity was significantly higher in the wetter half of the year, July–December (Tables III & IV).

Although short-term differences occasionally were noted, I found no significant difference in overall mean intensity between adult males and adult females (Tables III & IV). The adult class had a significantly higher mean intensity than the juvenile class. The juvenile 1 and juvenile 3 stages showed no significant difference in mean intensity, in spite of a considerable difference in body size (Tables III & IV). (Prevalence, however, was significantly lower in the juvenile 1 relative to juvenile 3 stage). Both the adult and juvenile classes had a significantly higher mean intensity than the infant class (Tables III & IV). I noted a steady increase in prevalence and mean intensity moving from the tiny and dependent infant 1 stage on through the infant 2 and 3 stages and, to a lesser extent, through the three juvenile stages (Table III). Relative density for each class in combined monthly data is compared in Fig. 4.

In general, monkeys tended to host no or few larvae (Table V). However, occasionally, monkeys were observed with as many as 18–20 larvae (Table III). Such high larval burdens were rare. Over the total sample period, only 40 monkeys were observed with ⩾12 larvae, 30 adults and 10 juveniles. High larval burdens were more common during the latter (rainy) half of the year (26 vs. 14). The single year with the greatest number of high infestations was 1989 which had 19 monkeys with ⩾12 larvae, 13 adults and 6 juveniles. Fifteen of these 19 cases occurred during the wetter period of the year. In hand-capture data (N = 135 monkeys), the highest number of larvae recorded for a single individual was 24.

Howler population parameters

Between 1977–1993, censusing data indicate that the BCI howler monkey population oscillated around a mean size of 1200 monkeys, at times exceeding and other times falling below this number but then returning again to this approximate size; graphed data showed some

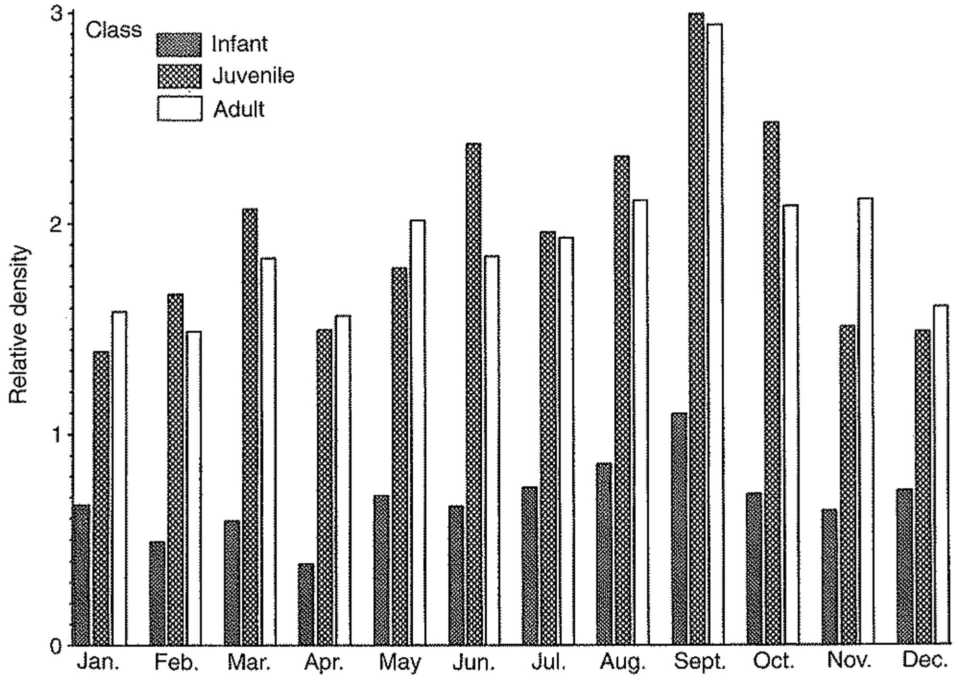

FIG. 4. Relative density of larvae by age class in combined monthly data for the total sample period. Adult, ⩾5 yrs of age, juvenile ⩾ 1 yr, <5 yrs, infant ⩽1 yr. Sample size per class = 2832 adults, 1316 juveniles, and 1348 infants. N = 5 months of data for February through May and 6 months of data for all other months except December where $n = 7$ months.

TABLE V

Percentage of total howler monkey sample infested with different numbers of larvae by class, by sex (if adult), and by stage (if immature)

		Number of larvae				
Class*		None	1–3	4–6	7–9	≥10
Adult	%	35.5	46.8	12.4	3.2	2.1
	N	1005	1326	350	91	60
Juvenile	%	27.7	54.6	13.1	2.8	1.8
	N	365	718	172	37	24
Infant	%	62.6	33.3	3.2	0.7	0.2
	N	844	449	43	10	2
Class-Sex						
Adult male	%	36.4	45.4	12.3	3.7	2.3
	N	483	603	163	49	30
Adult female	%	34.6	47.9	12.8	2.8	2.0
	N	525	727	194	91	31
Class-Stage**						
Juvenile 3	%	19.2	63.6	11.9	3.0	2.3
	N*	82	272	51	13	10
Juvenile 2	%	25.7	56.2	13.7	2.5	2.0
	N	92	201	49	9	7
Juvenile 1	%	29.6	53.5	12.6	3.7	0.7
	N	89	161	38	11	2
Infant 3	%	36.2	53.6	8.3	1.9	0
	N	96	142	22	5	0
Infant 2	%	60.5	35.9	3.1	0.3	0.2
	N	389	231	20	2	1
Infant 1	%	87.4	12.6	0	0	0
	N	194	28	0	0	0

* As defined in **Methods**

** Stage Ns do not sum to Class N as not all infants or juveniles were classified as to stage in monthly censuses

suggestion of five-year cycles (Fig. 5). Average troop size (± S.D.) between 1977–1993 was 19.4 ± 6.3 monkeys; average troop composition for this same period was 3.1 ± 1.2 males, 8.6 ± 3.1 females, 2.5 ± 1.5 juveniles and 5.3 ± 2.4 infants. No correlation was found between estimates of howler population size and any larval parameter (i.e. prevalence, mean intensity, relative density), but this result is based on only limited sampling of population size.

Without direct observation of births, the overall level of fertility can only be estimated indirectly. The simplest measure of fertility available is the ratio of infants to adult females (mean fertility rate) which in this case, extrapolating from censusing data for 1977–1993, is estimated at 0.64 (i.e. 64 infants for every 100 adult females). Some infants die, so the number born in a year would be greater than the number observed. With approximately 500 adult females in the population at any given time, on average, something over 320 infants would be born per year. These numbers are consistent with what is known about interbirth intervals. The estimated fertility rate varied depending on the month and year of the census, ranging from a low of 34.3 in February of 1990 to a high of 86.0 in December 1978. Even the most conservative estimate, however, suggested that > 200 howler monkey infants were born on BCI in each year of the censusing period (see also Milton, 1982). As the howler monkey population is closed and has not shown any persistent increase in size in the past 20 years, it would appear that mortality is high.

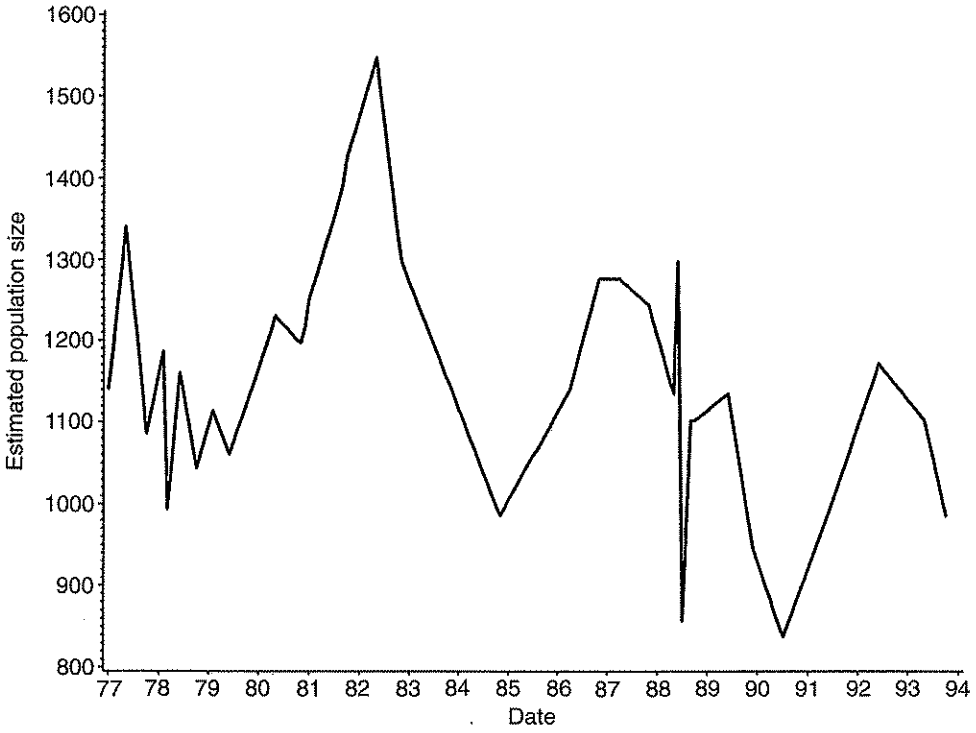

FIG. 5. Estimated size of the BCI howler monkey population as calculated from means of one or more troop censuses per year carried out between 1977–1993. Each census included ≥5 howler monkey troops. Within this period, seven years had only a single census month, one year, 1988, had six and one year, 1985, had none. Other years had from two to five monthly censuses. A total of 60 howler monkeys troops was consistently used for all estimates of population size.

Howler mortality

Between June 1986–Dec. 1993, a total of 203 howler monkey cadavers was found in the BCI forest (Fig. 6). In a few cases, the cause of death was septicemia due to the massive destruction of body tissue by screwworm and perhaps other flesh fly larvae. Screwworm larvae appeared to have entered the body of the monkey through a wound, often in the foot or hand and, in such cases, by the time of death, the entire appendage had usually been eaten away, such that only bones remained. In most cases, however, the cause of death could not be determined even on rare occasions when a cadaver was fresh enough for autopsy. Autopsy reports typically remarked on the high number of bot fly larvae and absence of fat reserves in cadavers. For example, autopsy of one young juvenile estimated to be 14 months of age (recently weaned) noted a total lack of omental or subcutaneous fat, as well as 10 bot fly larvae, *in situ* and healing warbles suggesting the very recent evacuation of as many as eight other larvae (Necropsy report #M-2880; N. B. Gale, DVM). Autopsy of another juvenile, estimated to be approximately three years old, showed 11 recently healed bot fly lesions on the chest and ventral cervical region, as well as extensive damage from screwworm and other flesh fly larvae; no subcutaneous fat was noted on the cadaver (Necropsy report #M-3254; N. B. Gale, DVM).

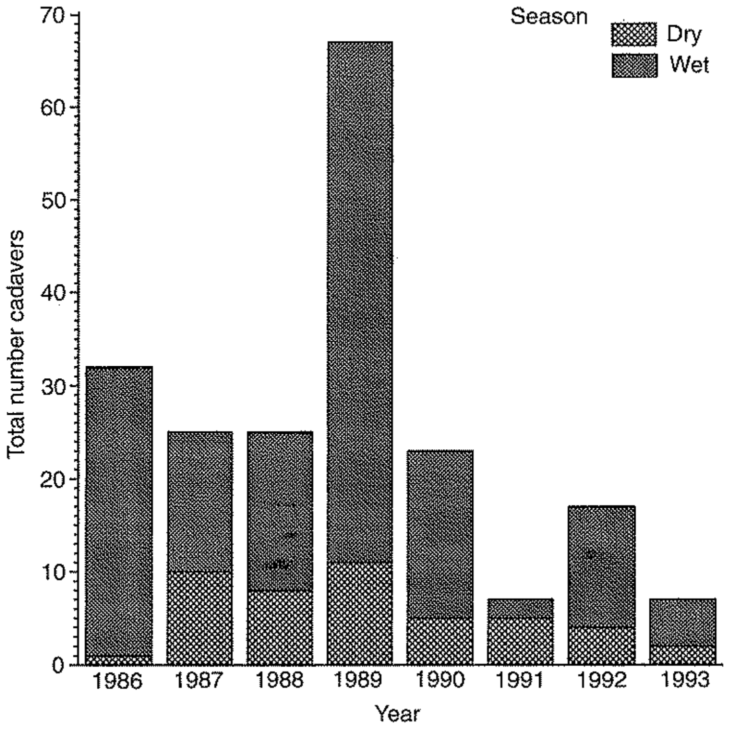

FIG. 6. Total number of howler monkey cadavers recovered from the BCI forest between May 1986 and December 1993 ($n = 203$ cadavers). Lighter hatching indicates cadavers found during the six months in the drier half of the year, Jan.–June ($n = 46$ cadavers), while darker hatching indicates cadavers found during the six months in the rainy half of the year, July–December ($n = 157$ cadavers).

Cadavers of adult monkeys were found more frequently than those of immature monkeys (Fig. 7). In my view, there is an unavoidable bias against finding cadavers of younger monkeys because of their small size and more fragile skeletal material (Milton, 1990). Furthermore, though 84% of the cadavers were found by individuals carrying out regularly scheduled activities in the BCI forest, it is not my intention to suggest that these were all, or even most, of the howlers that died during the study period. However, the monthly and seasonal distribution of deaths reflected in these data is regarded as accurate—the bounty I pay is sufficient to ensure that most or perhaps all dead howlers found are reported.

As shown in Figure 6, considerably fewer cadavers were found between 1991–1993 than 1986–1990. This difference appears due to a change in protocols in the Hubbell and Foster 50-hectare forest inventory plot on BCI. In each year between 1986–1990, all 50 hectares of the plot were routinely examined, a procedure which ensured that most howler remains both in and adjacent to this large plot, as well as on trails leading to it, would be found by Hubbell-Foster personnel. Sampling protocols for this project were modified in 1991 such that personnel spent less time in the plot (R. Foster, pers. comm.) and encounters with cadavers showed a decline. Both the 1986–1990 and the 1991–1993 data are regarded as valid representations of overall encounters with dead monkeys for each year in its set—but as

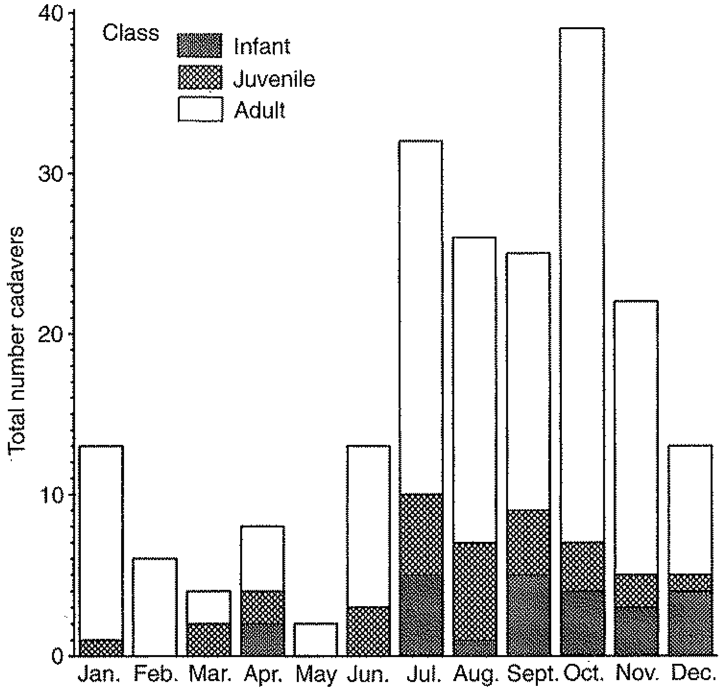

FIG. 7. Total number of howler monkey cadavers recovered in the BCI forest in combined data between May 1986–December 1993. Shading gradations indicate the number of individuals of each age class recovered.

the earlier set results from more detailed, continuous monthly surveys, it shows a higher number of recoveries.

The mortality pattern was similar from year to year. Few cadavers were found during the drier six-month portion of the year; however, once the rains began in May and June, the number of cadavers increased (Fig. 7; see also Milton, 1982, 1990). Mortality was significantly higher in the wetter six months of the year (Mann–Whitney U-test; $Z = -3.323$, $P < 0.0009$, $n = 43$ months Jan.–June, 48 months Jul.–Dec.). Combined data showed significant differences between months in the number of dead monkeys recovered (Kruskal-Wallis test; $\chi^2 = 25.85$, $d.f. = 11$, $P < 0.006$). Overall, October showed the highest mortality, followed by July and August (Fig. 7). Monthly mortality showed a strong positive correlation with prevalence (Spearman rank test; $r_s = 0.326$, $P = 0.006$, $n = 68$ months of data for mortality and prevalence) and relative density ($r_s = 0.293$, $P = 0.015$, $n = 68$ months of data for mortality and relative density) and a weak but significant correlation with rainfall ($r_s = 0.203$, $P = 0.053$, $n = 91$ months of data for mortality and rainfall). This latter correlation may only secondarily be related to mortality, perhaps reflecting the influence of rainfall on some other factor of importance to howler monkeys such as food abundance. No correlation was found between mortality and mean intensity ($r_s = 0.209$, $P = 0.088$, $n = 68$ months of data for mortality and mean intensity).

The association between mortality and relative density was shown most clearly in 1989. In 1989, prevalence and mean intensity rose in May and stayed high for the rest of the year, while unusually high mortality was first noted in June, that is, early in the rainy season, and continued to be high through December (Fig. 6). Between June and December 1989, 15 infants and six juveniles were found dead in the forest. The highest number of dead infants recovered in any other year was six in 1988, while for juveniles this figure was three (in 1986 and 1990). Adult cadavers also increased dramatically over other years in 1989 (46 cadavers recovered in 1989 vs. 27 in 1986, the year with the second highest mortality).

Census data for August 1989 and February 1990 (Table VI) showed that significantly fewer infants were present in February (Mann–Whitney U-test; $Z = 2.529$, $P < 0.01$). In August, 28% of the infants were neonates (infant 1 stage), younger than eight weeks of age; in February, the corresponding figure for neonates was 48% (Table VI). Neonates are light tan in colour and therefore unmistakable as older infants, juveniles, and adult howlers are black. When neonates are subtracted from the total number of infants present in February 1990, most of the remainder should represent older infants born the preceding year. In August 1989, older infants were estimated to make up 19% of the total population, while in February 1990, this figure was 8%.

Data on fruit production in 1989 were compared with similar data for 1988 and 1990 to see if evidence of a fruit shortage could be documented that might help to explain the high mortality in 1989. There was no significant difference in fruit production between the three years (Friedman two-way analysis of variance, $d.f. = 2$, $P = 0.701$; 85 most productive species considered in analysis). I censused monkeys on BCI in January and August of 1989 and February of 1990 and noted no evidence of disease or pathology. The only unusual features I noted in 1989 were the early onset and continuous presence of unusually high numbers of bot fly larvae in the howler population and the early and continuous recovery of an unusually large number of howler monkey cadavers.

Discussion

Because *A. baeri* is strongly dependent on howler monkeys for rearing larvae, one might assume that its effects on howlers would be negligible. Although studies of some bot fly species suggest that larvae do not harm the host (e.g. Dunaway *et al.*, 1967; Timm & Cook, 1979; Munger & Karasov, 1991), other studies suggest harmful or fatal effects (Dalmut, 1943; Sealander, 1961; Wecker, 1962; Payne *et al.*, 1965; Dunaway *et al.*, 1967; Miller & Getz, 1969). Various studies of bot fly-host interactions suggest a relationship between increased host mortality and size of the larval burden (Dalmut, 1943; Wecker, 1962; Miller & Getz, 1969). Munger & Karasov (1994), in their work with white-footed mice (*Peromyscus leucopus*),

TABLE VI

Comparison of troop census data in August 1989 and February 1990

	August 1989	February 1990
Mean troop size ($\bar{x} \pm 1$ S.D.)	19.4 ± 5.7	15.5 ± 5.3
No. troops counted	8	11
% contributed by juveniles to total	14	11
% contributed by infants to total	26	16
% contributed by neonates (0–2 months) to infant class	28	48
% contributed by older infants (>2–12 months) to total	19	8

estimated that, although costs to mice of hosting a single bot fly larva appeared low, costs could rapidly escalate with increasing larval burden.

The growth pattern shown by bot fly larvae lends support to the view that their effects on hosts can be harmful. Some 86% of larval growth occurs during the last week of the third instar when energy conversion is estimated at 95% and food consumption by the host increases by an average of 20% (Smith, D. H., 1978; Catts, 1982). This growth pattern suggests a strategy whereby the larval parasite is attempting to extract the maximum possible expenditure from the host at the last possible moment. Even if the final growth spurt of larvae kills the host, larvae should still be able to pupate successfully. The three-month interval between peaks in larval density noted for some years of this study, intervals which correspond to the life cycle of the parasite, likewise suggest that *A. baeri* larvae can kill or badly compromise their hosts. Entering hosts as a temporal cohort should help to ensure that early instars of one generation do not become trapped in moribund hosts weakened by the recent third-instar growth of a slightly earlier generation of larvae.

Although in this study, some significant differences in prevalence and mean intensity occurred between howler age classes, in my view this does not indicate that bot flies selectively parasitize any one age class (or stage or troop or individual howler monkey) on BCI. Rather, such differences are suggested to relate to as yet unknown characteristics of particular age classes (e.g. Anderson & Gordon, 1982; Theis & Schwab, 1992). The gradual increase in prevalence and mean intensity with increasing age that I noted in the infant and, to a lesser extent, juvenile classes, suggests a possible relationship between these features and host body size and/or independent movement away from the mother. It could also indicate, however, that younger hosts with multiple larvae suffer high mortality and generally are not counted in samples (e.g. Zhang *et al.*, 1993). The high prevalence that I noted in the juvenile class could relate to their higher activity levels relative to other classes (Milton & Leydorf, unpubl. data; see also Jacobson *et al.*, 1978), behaviour which could increase the probability of contact with bot fly larvae.

An aggregated distribution pattern seems characteristic of bot fly larvae regardless of species or locale (Pelton, 1968; Breyev & Minar, 1976; Minar, 1986). Because *A. baeri* deposit eggs in clusters, hypothetically, any contact between individual monkeys and larvae should result in many rather than one or few larvae gaining access to the host. Furthermore, though generally no more than 10% of the larvae in an egg cluster emerge simultaneously, a given howler monkey could come into contact with many different egg clusters in a short period of time and perhaps be infected with dozens of larvae. Yet combined field and capture data on more than 5000 monkeys showed no individual with >24 larvae and the great majority with <10. This suggests that some factor(s) is acting to set an upper threshold on the number of larvae that can establish on a given host at any one time.

Experimental work with cattle and bot fly larvae shows that, regardless of how many first instar larvae are simultaneously introduced into a potential host, only a small percentage actually become established (i.e. survival of the larvae to the hypodermal stage is density-related); there is also a negative relationship between high larval numbers in a host and percentage larval survivorship (Weintraub, McGregor & Brundrett, 1961). Antibodies in sera of howler monkeys may be an indication that some degree of protection is acquired through multiple infestation (acquired resistance), which may influence future attacks. As noted, the response appears to be directed at first instar larvae (Baron, Colwell & Milton, In prep.). I hypothesize that howler monkeys, like cattle, may have immune responses that limit the number of larvae that can establish at any one time. Differences between monkeys in their ability to mount an effective immune response, in turn, could affect the number of larvae per monkey. Body size may also play a role in setting limits to the number of larvae that can establish at any one time, perhaps because of active competition between early instars for resources and space.

Body size may also make it more difficult for young monkeys to meet costs of hosting larvae than adults. Weights for the infant 1 to juvenile 2 stage in howlers range from 300 to 3700 g. In contrast, the average (± S.D.) weight of an adult male howler is 8.1 ± 0.5 kg ($n = 13$) while that of an adult female is 6.6 ± 0.6 kg ($n = 26$). Yet many immature monkeys carry larval burdens equal to or greater than those of adults. Because of their larger body size, adult monkeys require less energy per unit mass than immature monkeys. Gut volume, however, scales in proportion to body size (Parra, 1978; Demment & Van Soest, 1985). Young monkeys therefore have higher energetic requirements per unit mass than adults, but a proportionately smaller gut volume to meet these accelerated demands. During the late rainy season on BCI, energy-rich plant foods, such as ripe fruits, are in short supply, as are protein-rich young leaves (Milton, 1980, 1982, 1991; Foster, 1982*a*, *b*). At such times, howler monkeys may live for days or weeks on diets consisting primarily of leaves (Milton, 1980, 1990), a diet in which larger body size confers decided energetic and nutritional benefits (Parra, 1978; Demment & Van Soest, 1985). When living on leaves, the energetic demands of howlers are met in part by volatile fatty acids produced in the fermentation of plant cell wall material (Nagy & Milton, 1979; Milton & McBee, 1982). The fat reserves of monkeys may also assume critical importance at this time of year (Milton, 1980).

Detailed study of the fat deposits of free-ranging cottontail rabbits (*Silvilagus floridanus mallarus*) showed a significant difference in the quantities of fat present between young and adult rabbits; low fat deposits in juveniles were attributed to high haematopoietic activity in the marrow of the growing young rabbits (Pelton, 1968). This study also found a dramatic and significant depletion of fat in rabbits parasitized by bot fly larvae (*Cuterebra* sp.), with lowest marrow fat derived from subjects with the greatest number of larvae (Pelton, 1968). A similar negative relationship between the amount of fat deposited in the host and parasitic infection has also been reported in a number of other studies (e.g. Crompton, 1987, 1991; Schall, 1983*a*, *b*; Mulvey, Aho & Rhodes, 1994).

If the negative relationship between fat reserves and parasitic infection found in other studies is also the case in howler monkeys, monkeys should be most affected by larvae during the mid-to-late rainy season when any fat reserves presumably are needed to help meet daily energetic requirements. During this period, costs associated with bot fly larvae that appear tolerated by many individuals earlier in the year when environmental conditions are more productive, might prove too high for some individuals. Recently weaned juvenile monkeys, in particular, might be unable to support such costs as well as satisfy their own energetic and nutritional requirements when living on diets composed primarily or exclusively of leaves. Old monkeys with badly worn dentition might not be able to reduce leaves to a particle size appropriate for adequate fermentation returns (e.g. Sinclair, 1977). Lactating females might be particularly vulnerable to energetic stress at this time of year due to the high costs of milk production. Exposure to bot fly larvae could increase such stress (Smith, C. C., 1977; Nagy & Milton, 1979; Munger & Karasov, 1994), perhaps forcing some females to abandon infants. Each year, abandoned infant howler monkeys are heard calling and observed alone in the forest, almost always during the late rainy season, but occasionally earlier as well.

Studies of white-tailed deer show that parasitic infections become serious only when population density is high enough such that deer have reduced their food resources, resulting in poor physical condition. At such times, various parasites tend to occur at more injurious levels

(Fowler, 1987), presumably because the immune response of the deer has been compromised by the lack of food. Though on BCI, seasonality rather than increased population density typically reduces food availability each year, the end result for howler monkeys could be the same as that for deer. All else being equal, monkeys with low or absent fat reserves eating diets composed largely of leaves might be able to mount only a weak immune response to larvae relative to peers in better physical condition, thus facilitating the establishment of larger larval burdens. The added costs of higher parasite burdens, in turn, could further compromise the health of the host (e.g., Dunaway *et al.*, 1967: 49). Should howler monkey population size increase without a corresponding increase in higher quality foods, this presumably would only intensify such problems.

The haematologic analyses, all of which involved blood samples collected during the mid-rainy season, showed a significant inverse relationship between increasing parasite burden and decreasing serum albumin level. Parasitized animals often show a decrease in serum albumin (Coles, 1980). Low albumin levels are indicative of a disruption of protein metabolism which can result from a number of causes including starvation, protein malnutrition, or the decreased synthesis of albumin in the liver (Coles, 1980). Decreased synthesis of albumin in the liver and a decrease in serum albumin concentrations have been documented secondary to inflammation (Liao, Jefferson & Taylor, 1986; Moshage *et al.*, 1987). The inflammatory response induced by bot fly larvae may suppress albumin synthesis in the liver and lead to low serum albumin levels due to the loss of albumin through exudation into the bot lesions (Liao *et al.*, 1986; Moshage *et al.*, 1987; N. Lerche, pers. comm.); some albumin may also be ingested by bot fly larvae. Payne *et al.* (1965) have suggested that bot fly larvae ingest albumin, bringing about a reduction in albumin/globulin ratio. After larvae leave the host, the poor nutritional conditions prevailing during the late rainy season could then prolong the period necessary to restore normal albumin levels. The requirement to restore albumin levels could theoretically add to the seasonal effects of nutritional stress on the population.

Unlike temperate regions, where bot fly larvae tend to be active for only one discrete portion of the annual cycle, in Panama successive generations of bot fly larvae persistently infect a moderate to sizeable percentage of the howler monkey population month after month, year after year. Possible effects of persistent exposure of some individuals to larval infection were shown most clearly in 1989 when prevalence and mean intensity were high from May through December, with >90% of the sample population infested in some months. By the mid-rainy season, monthly prevalence data showed that many monkeys must have been repeatedly infested. Fat reserves as well as immunological defences may have been completely exhausted in many individuals with the result that an unusually high number of howler monkeys, including numerous immature individuals, died throughout the rainy season in that year.

I conclude that primary and secondary effects of bot fly parasitism have played an important role in the demography of the BCI howler monkey population over the past two decades. Future work which focuses on the long-term monitoring of specific infants, juveniles, and adults, and documents their history of larval infection over time will help to test this hypothesis, as will study of the interplay between nutritional factors, larval burdens, and howler monkey physiology.

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