Intrinsic rate of natural increase of *Brueelia amandavae* (Ischnocera, Phthiraptera) populations infesting Indian red avadavat

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Abstract: The incubation period of eggs, duration of three nymphal instars, adult longevity and the daily egg-deposition rate of the ischnoceran Phthiraptera, *Brueelia amandavae*, were determined by rearing the louse *in vitro* ($35 \pm 1\,°C$, 75–82% RH, feather diet). The data obtained were utilized for life table construction and determination of the intrinsic rate of natural increase (0.031 per day) and the doubling time (23.45 days) of the louse population. The doubling time of the louse in *in vivo* experiments was 21.5 days.

Key words: Phthiraptera; biology; life cycle

Introduction

The intrinsic rate of natural increase (rm) of avian lice populations deserves investigation. Attempts to determine the values of rm of two mammalian lice, the sheep louse *Bovicola ovis* Schrank, 1781 and the rodent louse *Geomydoecus oregonus* Price et Emerson, 1971, have been made by Murray & Gordon (1969) and Rust (1974), respectively. As far as the avian lice are concerned, information on trends in population increase of the chicken body louse, *Menacanthus stramineus* Nitzsch, 1818 can be derived from papers of Glees & Raun (1959), Stockdale & Raun (1965) and Brown (1970). Recently, the intrinsic rate of natural increase of the poultry fluff louse, *Goniocotes gallinae* (De Geer, 1778) has been studied by Saxena et al. (2006, in litt.).

In the present paper, a life table was constructed and the intrinsic rate of natural increase was determined in the ischnoceran Phthiraptera, *Brueelia amandavae* Rekasi et Saxena, 2005, infesting red avadavat, *Amandavae amandavae* L., 1758 (Estrildidae), on the basis of data obtained during *in vitro* rearing. In addition, the doubling time of the louse population was calculated on the basis of data obtained from both *in vitro* and *in vivo* experimentation.

Material and methods

Feathers of red avadavat bearing freshly laid *B. amandavae* eggs were selected and placed in culture vials (small Petri dishes/ beakers, lined with black paper). The mouth of each culture vial was covered with muslin cloth and tied with a rubber band. The culture vials were then transferred to a 1000 ml battery jar/desiccator. Relative humidity was regulated in the desiccator/battery jar by placing 100 ml of a saturated salt solution as described by Winston & Bates (1960). The desiccator/battery jar was then placed in an incubator (fitted with digital temperature indicator cum controller)/B.O.D. incubator, maintained at the intended temperature. The culture vials were examined daily to record the hatching rate and the incubation period of the eggs. First instars of *B. amandavae* were further reared till the final moult (emergence of adult) to record the duration of the three nymphal stages. Feathers taken from abdominal/breast regions of the host body (preferred sites infested by the louse) were used for *B. amandavae* rearing. An examination of crop contents of several specimens revealed that it is a feather feeder, as its crop is always packed with feather barbules, arranged in lengthwise manner.

In a similar way, freshly moulted healthy adult lice were selected and transferred to culture vials (glass beakers, without spout). The latter were placed in a desiccator/battery jar as described above. Culture vials were examined daily to record oviposition and mortality. All feathers in the culture vials were not changed regularly, but those carrying fresh eggs were replaced (by feathers devoid of eggs). A hot plate (thermo-statically controlled) was used as a heat source, when the lice were removed from the incubator for the purpose of data recording, change of feathers and the removal of exuvia.

The life table of *B. amandavae* was constructed based on the guidelines given by Birch (1948), Leslie & Park (1949), Evans & Smith (1952) and Howe (1953). The intrinsic rate of natural increase (rm) was determined by the

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Table 1. Survival and oviposition rate of freshly moulted adults of *Brueelia amandavae*, reared at 35 ± 1 ℃, 75–82% RH, on a feather diet.

Composition	Colony "A" 30 M : 30 F	Colony "B" 30 M : 30 F	Colony "C" 30 M : 30 F	Average –
Adulf lifespan (male) in days (mean ± SD)	9.83 ± 3.31 (range 3–14)	9.90 ± 3.76 (range 2–15)	10.53 ± 3.88 (range 3–16)	10.08 ± 3.67 (range 2–16)
Adult lifespan (female) in days (mean ± SD)	14.20 ± 5.56 (range 2–21)	12.20 ± 4.47 (range 3–19)	12.74 ± 5.10 (range 2–21)	12.74 ± 5.10 (range 2–21)
Total number of eggs produced	162	156	175	493
Number of eggs produced during female lifespan	5.40	5.20	5.80	5.40
Eggs laid/female/day	0.49	0.60	0.65	0.53

equation:

$$\sum e^{-rm\,x}lx\,mx = 1$$

where e is the base of natural logarithm, x is the age of individuals in days, lx is the number of individuals alive at age x, as a proportion of 1 and mx is the number of female offspring produced per female in age intervals x.

The value of mx was determined by multiplying the daily average egg rate by a factor of 0.58 (as the male : female ratio in the natural population of *B. amandavae* was 1: 1.38 (Gupta et al. 2006, in litt.). The sum of products of lx and mx ($\sum lx\,mx = Ro$) was regarded as the net reproductive rate (indicating that one living female egg would be, on average, replaced by Ro living daughter eggs). Practically, the time interval between the birth of a parent and the birth of a parent's offspring is referred to as the generation time. However, the generation time is different for each individual parent, so theoretically the value of cohort generation time (Tc) was calculated by the equation: $Tc = \sum x\,lx\,mx/Ro$ (Evans & Smith 1952). The definite rate of increase (λ) was determined as e^{rm} (natural antilogarithm of rm). Finally, the doubling time was calculated by the equation: $DT = \log 2/\log \lambda$.

In vivo studies were performed by inoculating louse free birds with a known louse population. Two adult males and three adult females (freshly moulted) selected from the culture stock were released on each of ten louse free birds. Camel hairbrush was used for transferring the lice. The infested birds were kept in five cages (two per cage) up to 2½ months, by providing similar food and other conditions. To recover the louse load, two birds were deloused fortnightly, firstly by fumigation and then by visual examination (under stereozoom trinocular microscope). The doubling time (*in vivo* condition) was computed by the back roll method.

Results and discussion

The mean duration of the incubation period of 81 eggs (of 95 eggs incubated in 3 batches at 35 ± 1 ℃, 75–82% RH) was 5.81 ± 0.80 (mean ± SD) days (range 5–7 days) (Fig. 1). Of these, a total of 63 first instars moulted into second instars, with a mean duration of 6.84 ± 0.88 days (range 6–9 days). Likewise, 40 second instars moulted into third instars after 5.83 ± 0.77 days (range 5–7 days). The average duration of 17 third instars which moulted into adults (5 males and 12 females) was 5.65 ± 0.76 days (range 5–7 days).
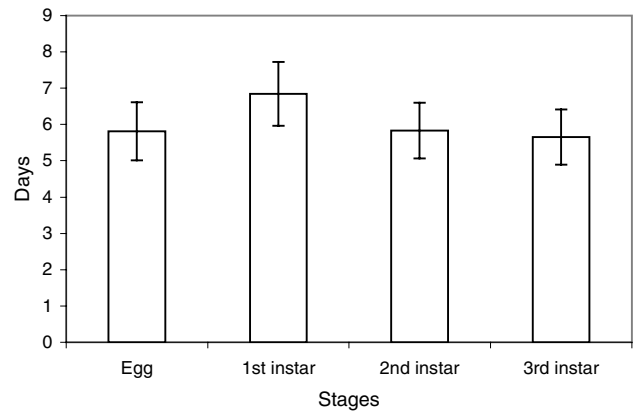

Fig. 1. Duration (mean ± SD) of different life cycle stages of *Brueelia amandavae* in laboratory (35 ± 1 ℃, 75–82% RH, feather diet).

The composition of the louse population, lifespan of adults, number of eggs produced per female during its lifespan and the egg laying rate of each colony (reared at 35 ± 1 ℃, 75–82% RH, on a feather diet) are shown in Table 1, along with the pooled average. The average lifespan of male and female *B. amandavae* was 10.08 ± 3.67 days (range 2–16 days, $n = 90$) and 12.74 ± 5.1 days (range 2–21 days, $n = 90$), respectively. A total of 493 eggs were laid in three colonies. Thus, an adult female laid on average 5.40 eggs during its lifespan at a rate of 0.53 eggs/female/day.

Based on the data on incubation period of eggs, duration of nymphal instars, pre-oviposition period, age specific mortality/survivorship and fecundity, a life table was constructed (Table 2, Fig. 2). The gross reproductive rate ($\sum mx$ – average number of daughter eggs expected to be produced by a female living throughout the entire reproductive period) was 4.98. The net reproductive rate (Ro) was 3.13, indicating that a living female egg would, on average, be replaced by approximately three living daughter eggs, i.e., a three fold increase per generation. The mean duration of a generation ($\sum x\,lx\,mx/Ro$) was 35.40 days. The intrinsic rate of natural increase was estimated by using the trial values of rm to find out the value which will fit the equation $\sum e^{-rm\,x}lx\,mx = 1$. With the value of $rm = 0.031$, the summation of $e^{-rm\,x}lx\,mx$ proved to

Table 2. Life table, fecundity and rate of increase of Indian red avadavat louse population, *Brueelia amandavae*.

| Mid point of age class (in days) (x)	Number of female lice	Age specific longevity (lx)	Eggs per female per day	Number of females produced per female (mx)	$lx\,mx$	$x\,lx\,mx$	$rm\,x$	$e^{-rm\,x}$	$e^{-rm\,x}lx\,mx$
0–24.5	Immature stage of *Brueelia amandavae*								
25.5–26.5	Pre-oviposition period								
27.5	90	1.00	0.00	0.000	0.000	0.000	0.853	0.426	0.000
28.5	86	0.95	0.00	0.000	0.000	0.000	0.884	0.413	0.000
29.5	84	0.93	0.10	0.058	0.054	1.591	0.915	0.401	0.022
30.5	82	0.91	0.41	0.238	0.216	6.600	0.946	0.388	0.084
31.5	80	0.88	0.61	0.354	0.311	9.807	0.977	0.377	0.117
32.5	80	0.88	0.70	0.406	0.357	11.612	1.008	0.365	0.130
33.5	75	0.83	0.70	0.406	0.337	11.289	1.039	0.354	0.119
34.5	71	0.78	0.67	0.389	0.303	10.457	1.070	0.343	0.104
35.5	62	0.68	0.79	0.458	0.312	11.061	1.101	0.333	0.104
36.5	62	0.68	0.64	0.371	0.252	9.213	1.132	0.323	0.081
37.5	57	0.63	0.59	0.342	0.216	8.084	1.163	0.313	0.067
38.5	46	0.51	0.67	0.389	0.198	7.630	1.194	0.303	0.060
39.5	45	0.50	0.60	0.348	0.174	6.873	1.225	0.294	0.051
40.5	36	0.40	0.66	0.383	0.153	6.201	1.256	0.285	0.044
41.5	34	0.37	0.58	0.336	0.124	5.165	1.287	0.276	0.034
42.5	30	0.33	0.36	0.209	0.069	2.928	1.318	0.268	0.018
43.5	18	0.20	0.33	0.191	0.038	1.665	1.349	0.260	0.010
44.5	11	0.12	0.18	0.104	0.013	0.557	1.380	0.252	0.003
45.5	5	0.05	0.00	0.000	0.000	0.000	1.411	0.244	0.000
46.5	3	0.03	0.00	0.000	0.000	0.000	1.442	0.237	0.000
47.5	1	0.01	0.00	0.000	0.000	0.000	1.473	0.229	0.000
Total				4.982	3.128	110.736			1.050
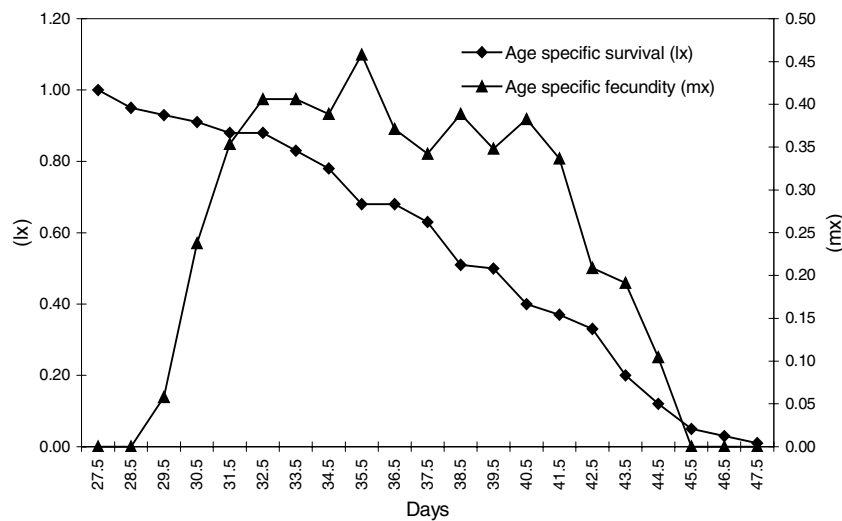
Fig. 2. Age specific survival and fecundity of *Brueelia amandavae* in *in vitro* conditions (35 ± 1 ℃, 75–82% RH, feather diet).

be 1.050 (Table 2, column 10), a reasonably good approximation to the formula. The final rate of increase in numbers ($\lambda = e^{rm}$) was 1.03. Thus, under the provided condition the population is supposed to double ($DT = \log 2 / \log \lambda$) after every 23.45 days.

During *in vivo* experiments, 22 lice (1 M, 2 F, 19 N) were recovered from two birds deloused after 15 days. The number of lice recovered after 30, 45 and 60 days was 44 (3 M, 3 F, 38 N), 53 (14 M, 19 F, 20 N) and 96 (22 M, 29 F, 45 N), respectively. Finally, the last two birds deloused after 75 days yielded 120 specimens of *B. amandavae* (15 M, 37 F, 68 N). Thus, the initial inoculum of five lice increased, on average, to 60 lice

per bird during the span of 75 days. By applying the back roll method, the doubling time of *B. amandavae* was estimated to be 21.5 days (Fig. 3).

Marshall (1981) has clearly pointed out that adequate information for construction of a life table for ectoparasitic insects is scarce. For instance, Evans & Smith (1952) presented the life table of *Pediculus humanus* L., 1758 (Anoplura) after making several assumptions and determined the intrinsic rate of natural increase (rm) as 0.111 per day (or doubling within 6.42 days). The mean generation length of *P. humanus* and the net reproductive rate were 30.92 days and 30.93 days, respectively. However, in case of the sheep louse,
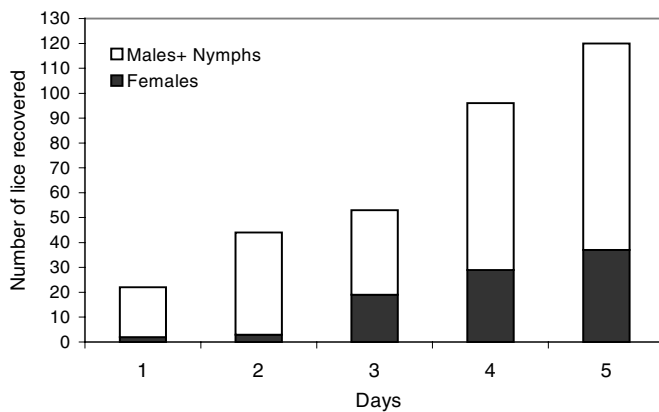
Fig. 3. Pattern of population expansion of *Brueelia amandavae* on the Indian red avadavat (initial population consisted of 2 male and 3 female lice).

B. ovis, the *rm* was 0.053 per day (thus, doubling within 13–14 days; Murray & Gordon 1969). The value of *rm* for *G. oregonus* was found to be 0.006 per day (thus, doubling after 112 days) (Rust 1974). In case of the poultry fluff louse, *G. gallinae,* the gross reproductive rate (13.53), net reproductive rate (11.53), mean length of generation time (36.10 days), intrinsic rate of natural increase (0.07 per day) and the doubling time (10.03) have been evaluated by Saxena et al. (2006, in litt.). The mean length of generation time of *B. amandavae* is nearly similar to that of *G. gallinae.* However, the values of the gross reproductive rate, net reproductive rate, intrinsic rate of natural increase and the doubling time are lower, indicating the low reproductive potential of this louse.

Studies on the rate of population expansion of avian lice have rarely been carried out in *in vivo* conditions. Glees & Raun (1959) released ten adult chicken body lice, *M. stramineus,* per each experimental poultry bird and found that their number increased to 23,063 lice per bird during a span of 14 weeks. In a similar way, Stockdale & Raun (1965) noted that three adult females of the same louse species produced 12,305 offspring within 16 weeks. Brown (1970) found that an initial population of 50 chicken body lice increased to 1,584 in 31 days on debeaked birds but the same numbers (50) released on beaked birds, could not increase beyond 56 lice, indicating that host preening has profound effect on the growth of the louse population. In

G. gallinae (Saxena et al. 2006, in litt.), the initial population of 14 lice (4 males, 10 females) produced 1,159 offspring in a 14 weeks interval. The doubling time of *G. gallinae* recorded through *in vivo* studies was 14 days, while in *B. amandavae* it was 21.5 days (*in vivo*), indicating slower rate of population expansion. This may be one of the reasons for the lower infestation intensity of *B. amandavae* (Gupta et al. 2006, in litt.).

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