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Adaptive strategy in control of ectoparasitic infection in Eurasian tree sparrow

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Abstract

Background: Selection pressure due to parasitic infestation puts adverse effects on birds' fitness concerning survival and reproductive success. The present study was conducted on Eurasian tree sparrow at Shillong (25°34' N, 91°53' E), India, for a year to examine ectoparasitic infestation by *Myrsidea balati* and *Sturnidoecus ruficeps*. The parameters on the annual prevalence of infestation, annual cycles of gonadosomatic index (GSI), molt, hematocrit percentage and the time spent in behavior display were recorded.

Results: The infestation of both lice species ran parallel to GSI in both sexes of sparrow. Further, the intensity of infestation was higher in males. The increase in number of ectoparasites was found positively correlated with the increase in GSI in the birds. However, it was negatively correlated with feathers molt. Thus, the infestation of both parasites was maximum during the reproductive phase and minimum during the period when the birds were undergoing the process of molt. Seasonal variation in hematocrit percentage shows decline during high infection in females and during molt in both the sexes. The time spent in showing behavioral traits to limit infection was the longest during high infestation.

Conclusions: We conclude that the tree sparrow adopts various adaptive strategies like feathers molt and longer display of behavioral traits during their breeding and/or non-breeding seasons to control parasitic load and avoid energy conflict with high energy demanding processes like reproduction and molt.

Keywords: Ectoparasite, Gonadosomatic index, Hematocrit, Molt, Tree sparrow

Background

The life-history stages of birds include reproduction, molt and migration (in a migratory species). These events are repeated in a cyclic manner every year. The overlapping of the above high energy demanding processes is generally avoided (Dixit & Singh, 2011; Dixit et al., 2017). The reproductive activity intensifies with the approach of the breeding season in most birds, and there is an increase in the parasite load along with it (Gibson, 1990). The presence of parasites brings a powerful selection pressure that affects both the survival and reproductive components of bird's fitness in the wild population

(Clayton & Moore, 1997). Nestlings are most vulnerable to ectoparasite infestation as they are sedentary and cannot preen effectively, and their immune system is not completely developed (Koop et al., 2015). The literature on the effects of ectoparasites on adult birds is scanty (Clayton & Tompkins, 1995; Puente et al., 2010). Moreover, it is unclear whether infestations can have long-term fitness costs, which is an important notion of many host-parasite interaction studies (Puente et al., 2010).

Of all the parasites, chewing lice (Insecta: Phthiraptera) is one that is of great concern to the health and survival of birds. They are ectoparasites that feed on feathers and cause heavy damage (Clayton, 1991; Vas et al., 2008) which may impair flight performance in the host (Barbosa et al., 2003). Their parasitic infection also induces irritation, allergy and destruction of tissue, which in turn causes scratching of the infected area adding additional

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damage to it (Philips, 2007). In addition, dense lice infection causes anemia (Hannam, 2006), low egg production (Moller, 1993), low developmental rate (Okaema, 1988), weight loss (Philips, 1990), selection pressure for mate choice (Moreno-Rueda & Hoi, 2012) and sleepless problems (Mansur et al., 2019) in birds. These parasites may also transmit epizootic diseases to the host (Bittencourt, 1995). They are mostly permanent parasites and complete their entire lifecycle in the hosts (Soto-Patino et al., 2018). Most of them are host specific (Price et al., 2003), and some are so specialized that they are restricted to only a particular area in the host (Clayton et al., 1999), while few show no habitat preference (Singh et al., 2011). Direct physical contact between the two hosts is required for their transmission (Price et al., 2003). However, like with other parasites, chewing lice have concentrated distribution to a particular area of the body and a low number of hosts shelter the majority of parasites in a given population (Viljoen et al., 2011). Further, the distribution often shows a sex-biased pattern with males accommodating greater number of ectoparasite than the females (Klein, 2004).

In general, hosts and parasites are in continuous engagement with each other. The parasites are expected to impose selection for host resistance, while hosts select for enhanced infectivity of parasites (Lars et al., 2014). This reciprocal selection can result in coevolution of host defense and parasite counter-defense mechanisms (Thompson, 2005). Birds seem to have evolved an extensive diversity of defense mechanisms for combating ectoparasites (Clayton et al., 2010). However, continuing resistance against parasites may be costly for hosts, compelling them to assign limited resources to defense rather than other life-history stages (Norris & Evans, 2000). Although the immune system plays an important major role in defense against ectoparasite infestation, the first line of defense against parasites is the behavior traits (Hart, 1990). One such behavior includes avoiding getting infected by lice in the first place (Clayton, 1991). Other behaviors include scratching by the middle claw, bathing, sunning, dusting and preening or oral grooming (Clayton et al., 2010). The defensive mechanism that has received less attention is the periodic replacement of worn feathers, i.e., molt (Moyer et al., 2002). There are reports that the molt reduces ectoparasite influx, in addition to substituting damaged feathers in birds (Lehane, 1991).

Most studies on ectoparasite infestation have been done on domestic birds (Okursoy & Yilmaz, 2002; Senlik et al., 2005). The data on the seasonality of avian lice infestation have been limited only to a few wild birds, i.e., feral pigeon (*Columba livia*) (Gollaway & Lamb, 2015) and woodpeckers (*Picoides pubescens*, *Sphyrapicus varius* and *Colaptes auratus*) (Lamb & Galloway, 2016), while

no report is available in the birds inhabiting the North-Eastern region of India, one of the biodiversity hotspot regions, having very different climates and geographical conditions from other part of the country. Therefore, in the present study, we planned to investigate ectoparasitic infestations of two chewing lice, i.e., *Myrsidea balati* and *Sturnidoecus ruficeps* which are ectoparasites on Eurasian tree sparrow (*Passer montanus*) at Shillong, a North-East part of India. Also, the seasonal prevalences of above infestation have been compared and correlated with the annual cycles of reproduction, molt, hematocrit percentage and time spent in display of behavioral traits aimed to reduce infestation. While *Myrsidea balati* feeds on both feathers and blood, *Sturnidoecus ruficeps* feeds only on host feathers. The above lice were chosen for the present study as they are very selective in host preference, stay permanently as they lack free-living stages and complete their life cycle in the host, i.e., tree sparrow. The tree sparrow is a resident bird found throughout the year at Shillong, Meghalaya, India. It has a chestnut crown, black throat and a black patch on white cheek. No sexual dimorphism was observed in this species (Sibley & Monroe, 1990).

Methods

Two experiments were performed on subtropical population of the tree sparrow. In the first experiment, adult birds of both the sexes were captured in the middle of every month of the year from their wild habitat in Shillong, Meghalaya, India, using mist nets. They were brought to the laboratory in cages covered with black cloth and allowed to stabilize for an hour which was followed by their sex identification. Observations on both the sexes were made to record. Body weight, gonadosomatic index (GSI), molt, hematocrit percentage, ectoparasite prevalence and percentage of infection. The birds were first weighed to record their body weight using a digital pan balance with a minimum detection range of 0.1 g. They were then screened for the presence of both the lice species (*M. balati* and *S. ruficeps*) by visual examination following the procedure adopted by Clayton and Drown (2001). These parasites were fixed in 70% ethanol and slide-mounted for their identification under microscope. Identification of the lice and their eggs was made as per Ansari (1958) and Singh et al. (2011). *M. balati* has a broad and large head and thorax in proportion to the abdomen. The ventral side of the rounded head lacks spines and the head seta 23 is missing. There is no preocular slit or notch, and sternites are with four strong spines and asters with spine-like setae. The presence of sclerite is in the genital region. Eggs are amphora shaped having an operculum and remain glued to the underside of the rachis of feathers. *S. ruficeps* has broad

temples and broadly oval abdomen. There is presence of sub-lateral row of normal setae in both male and female. The female sub-genital plate has a posteriorly pointed

pigmented part. Male genitalia are distinct with a little extra plurite in segment V. It has moderately developed calyx (Fig. 1). The data on presence of *M. balati* and *S.*

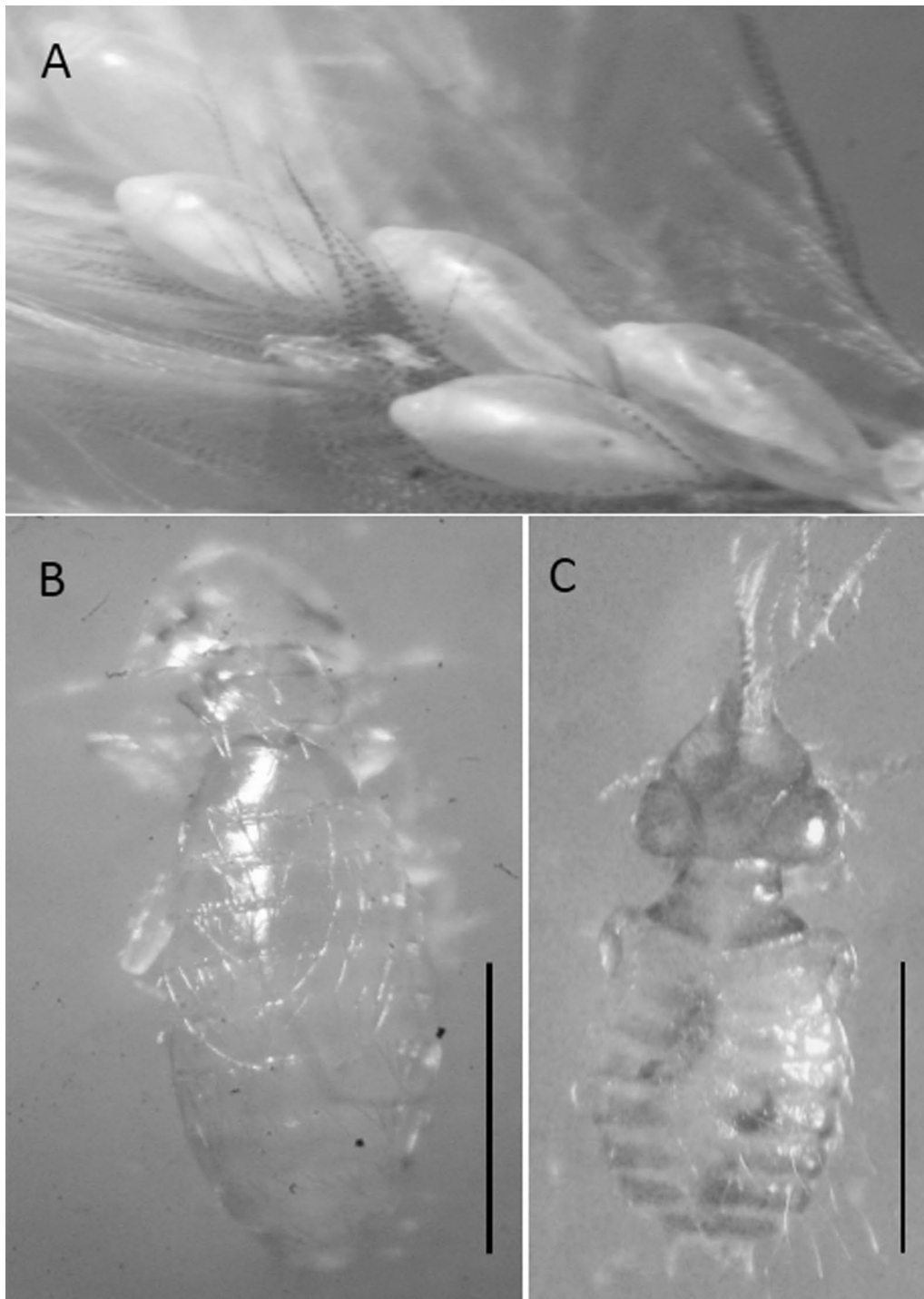


Fig. 1 A Amphora shape eggs of *Myrsidea balati* with an operculum, glued underside the rachis of feathers, photograph of (B) *Myrsidea balati* and (C) *Sturnidoecus ruficeps*. Line bar in 0.5 mm

ruficeps on male and female tree sparrows ($N=14$ each sex per month) were collected and analyzed separately. Two measures of ectoparasitic load were used in the present study, i.e., prevalence and percentage of infection. The ectoparasitic prevalence was found out by giving scores in a scale of 0–2. The detection of ectoparasite lice was given a score of 2. The presence of eggs was assigned a score of 1, while 0 score was given when no ectoparasite or egg was detected. The percentage of infection (PI) was calculated by dividing the number of infected birds (IB) by total number of birds (N) collected during each month and multiplying it by 100 ($PI = IB/N \times 100$). Molt, in these birds, was recorded by observation on body and wing feathers as per Budki et al. (2008) with some modification. For recording of feathers molt, the whole body of the bird was divided into 13 different regions as follows: 1 = head, 2 = neck, 3 = shoulder, 4 = back, 5 = pelvic, 6 = caudal, 7 = throat, 8 = chest, 9 = abdomen, 10 = flank, 11 = shank, 12 = sub-caudal and 13 = wing. Each region could have a score of either 0 (no molt, fully grown or old feather present) or 1 (molt: no feather or new feathers emerging), and hence, the total body molt score could be in the range of 0–13. For obtaining hematocrit percentage in the birds, their blood samples (50 μ l) were collected in micro-hematocrit capillary tube by puncturing the wing vein using a 26-gauge needle. This type of blood sampling has no risk to bird health (Dixit & Singh, 2014). One end of capillary tube was shielded, and the blood was centrifuged at 12,000 g for 5 min. The percentage of red blood cells in the capillary tube was calculated in terms of proportion between volume of red blood cells and the volume of the whole blood in the capillary tube after centrifugation as per the procedure adopted by Campbell (1994).

After recording of above observations, the birds were anesthetized by giving subcutaneous injection of 2% xylocaine (Astra-IDL Ltd. Bangalore, India; Dixit & Singh, 2013). Bilateral laparotomy was performed on the anesthetized birds by surgical opening of the abdominal wall between the last two ribs on both left and right sides, while unilateral laparotomy was done on the left side only for female. The gonad was located within the abdominal cavity with the help of a spatula, and the sex of the bird was identified. The gonadal weight was estimated by comparing gonad in situ with reference sets of the testes and ovaries of known weights preserved in vials. The estimated combined testicular weight of both left and right testes was considered in case of males birds, while only the left ovarian weight was estimated in case of females. An antibacterial ointment (soframycin, Aventis Pharma Ltd.) was applied on the wound after stitching. The gonadosomatic index (GSI) of these birds was calculated by

dividing their gonadal weight (GW) by body weight (BW) and multiplying it by 100, i.e., ($GSI = GW/BW \times 100$). The birds were then ringed with the date and place of collection encrypted on it and housed in an outdoor aviary. They were fed with food consisting of paddy (*Oryza sativa*), kakuni (*Setaria italica*) mixed in equal proportion and water *ad libitum*. These birds were finally released in their natural habitat after their full recovery. The occasionally caught ringed birds were excluded from the data analysis.

In the second experiment, total display time of various behavioral traits of sparrow ($N=12$ each months) such as bathing (soaking in water by flapping their wings and exposing their body and feathers to water), sunning (birds fluffed up the body feathers with one or both wings starched out from the body with spread feathers), dusting (cover their body feather with sand), preening or oral grooming (use of the beak to place feathers, interlock separated feather barbules, and clean plumage) and scratching (scratching the head, neck and other parts of the body with the claws) per hour of observation was recorded in their wild habitat using a binocular for three consecutive days in the middle of every month over a year during the morning (7 to 8 AM) and evening (2–3 PM) time. These observations were made from a safe and far distance to minimize the impact of presence of observer on their behavior. As there is no sexual dimorphism in tree sparrow, the above behavioral traits were recorded on individual birds without considering their sexual difference. Most of the behavioral traits of sparrows observed during the time of study overlapped with each other, i.e., sunning and preening, were going on simultaneously and while dusting they were also scratching. Therefore, the data on the duration of various behavior displays per hour were put together and presented as one in the present study. Monthly data on behavioral traits and parasitic infection were collected from the sparrows of same wild stock and habitat for their meaningful correlation.

Data from different experiments are presented as mean \pm SEM. Shapiro–Wilk's W test was used for the test of the normality of the data. They were then analyzed using general linear mixed model testing the effect of months, sex and interaction. The means were compared using Bonferroni post hoc test. Pearson correlation coefficient (r) analysis was used to see the relationship between the factors involved in the experiment. Significance was accepted at $P < 0.05$. The statistical analysis was done using SPSS software (version 20). All the experiments and animal care were carried out under the guidelines of the institutional animal ethics committee of the North-Eastern Hill University, Shillong, India (1886 of 04. 12. 2014).

Results

The gonadosomatic index (GSI) in both sexes of wild tree sparrow varied significantly over a year (month: $F_{11, 264}=277.4$, $P<0.0001$; sex: $F_{1, 264}=37.7$, $P<0.0001$ and interaction: $F_{1, 264}=20.5$, $P<0.0001$; two-way ANOVA; Fig. 2A). Although there was a slight increase in GSI in March, a significant increase was noticed only in April ($P<0.05$) that reached to peak in May ($P<0.001$). Thereafter, the GSI declined gradually ($P<0.001$) reaching to a minimum value in September which was maintained till December in both the sexes. The peak GSI in males was significantly higher as compared to females ($P<0.001$). A significant variation in feathers molt of both the sexes of tree sparrow was observed under wild conditions (month: $F_{11, 264}=213.4$, $P<0.0001$; sex: $F_{1, 242}=5.642$, $P=0.0183$ and interaction: $F_{1, 264}=3.159$, $P<0.0001$; two-way ANOVA; Fig. 2A). The feathers molt proceeded gradually with decline in GSI from June ($P<0.05$) that was steadily intensified reaching to maximum molt score in August ($P<0.001$). A decline ($P<0.05$) in body molt was noticed in September (males)/October (female) reaching to minimum in November in both sexes. Thus, the body molt in tree sparrow extended from June to November,

a period when GSI was declining or maintaining minimal levels. Both sexes displayed almost similar pattern of molt except that the decline in feathers molt was faster ($P<0.05$) in males (Fig. 2A). The presence of both the ectoparasites (*M. balati* and *S. ruficeps*) and their eggs in male as well as female tree sparrows showed a cyclic pattern running almost parallel to the GSI and antiparallel to the body molt (Fig. 2B). The prevalence scores of both the lice species increased gradually from February and reaching to peak in April and declining significantly ($P<0.05$) thereafter leading to its minimum score in June (*S. ruficeps* in females sparrow)/July (*S. ruficeps* in males and *M. balati* in both sexes of sparrows) which was maintained till September (months: $F_{11, 624}=23.74$, $P<0.0001$, sex: $F_{3, 624}=4.36$, $P=0.0051$ and interaction: $F_{33, 624}=0.7279$, $P=0.8689$; Fig. 2B). Although the presence of both the lice species was detected only in few birds captured from October to December, it was found to be insignificant. A distinct sex difference in the infection percentage as well as prevalence score of both the lice species was noticed in tree sparrow with greater infection percentage and prevalence score in males as compared to females (Fig. 2B and C). There was a positive correlation between the GSI of birds and the ectoparasite infection (*M. balati*: male— $r=0.5987$; $P=0.0397$; female— $r=0.6866$; $P=0.0133$ and *S. ruficeps*: male— $r=0.6722$; $P=0.0166$; female— $r=0.7091$; $P=0.0098$; Fig. 3A and B) suggesting a significant rise in ectoparasite infection with the increase in GSI. However, a negative correlation existed between molt and parasitic infection (*M. balati*: male— $r=-0.5797$; $P=0.0482$; female— $r=-0.6114$; $P=0.0347$ and *S. ruficeps*: male— $r=-0.5813$; $P=0.0475$; female— $r=-0.6068$; $P=0.0364$; Fig. 3C and D) when a declining trend in infection was noticed with progression of molt in both the sexes of tree sparrow.

Although there was a significant decrease in hematocrit % at the times of peak GSI and parasitic infection (female: April) and also feathers molt in both the sexes (male: July/August, and female: July) of tree sparrow, no correlation was observed between the ectoparasite infection and hematocrit % (male sparrow and ectoparasite score: $r=-0.1950$; $P=0.5437$; female sparrow and ectoparasite score: $r=-0.2646$; $P=0.4059$). Further, no sex difference was observed in the variation of hematocrit % in the tree sparrow. Tree sparrows showed significant ($F_{11, 143}=7.305$, $P<0.0001$; Fig. 4B) variation in the time spent by the different behavioral traits over a year. The durations of showing behavioral traits during the breeding period (January–May) with high GSI and parasitic infection were significantly longer ($P<0.05$) than during the non-breeding period (June–December) with low GSI and low parasitic infection. Further, there was an increase followed by decrease in the display time

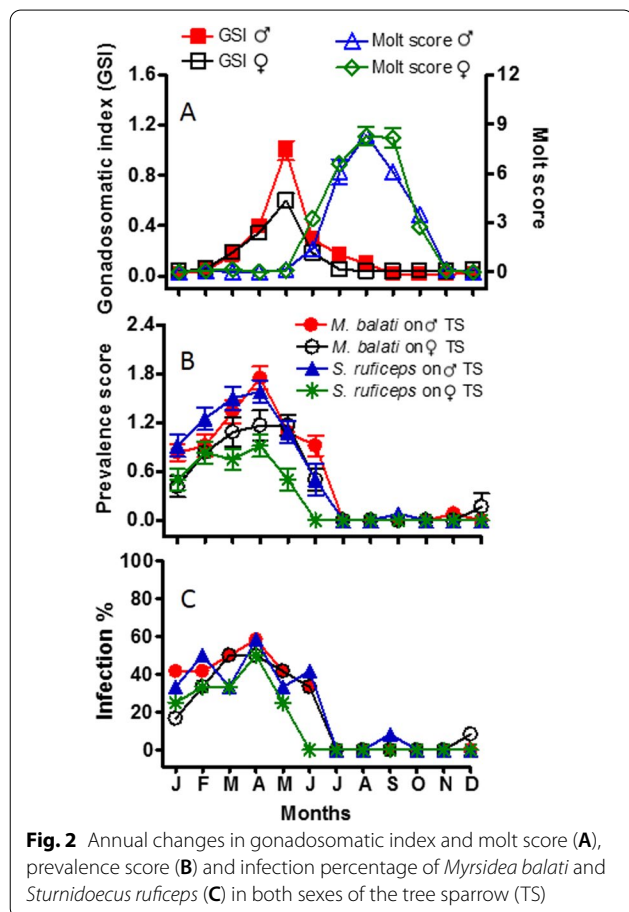
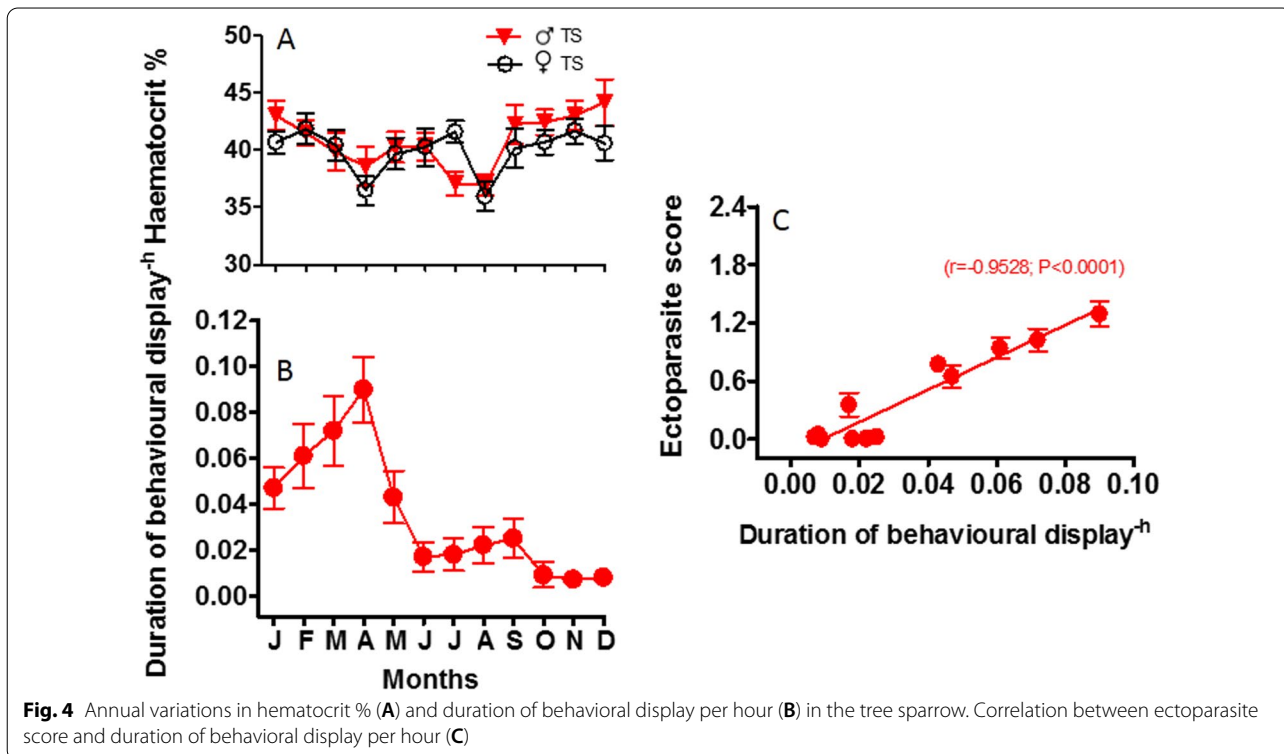
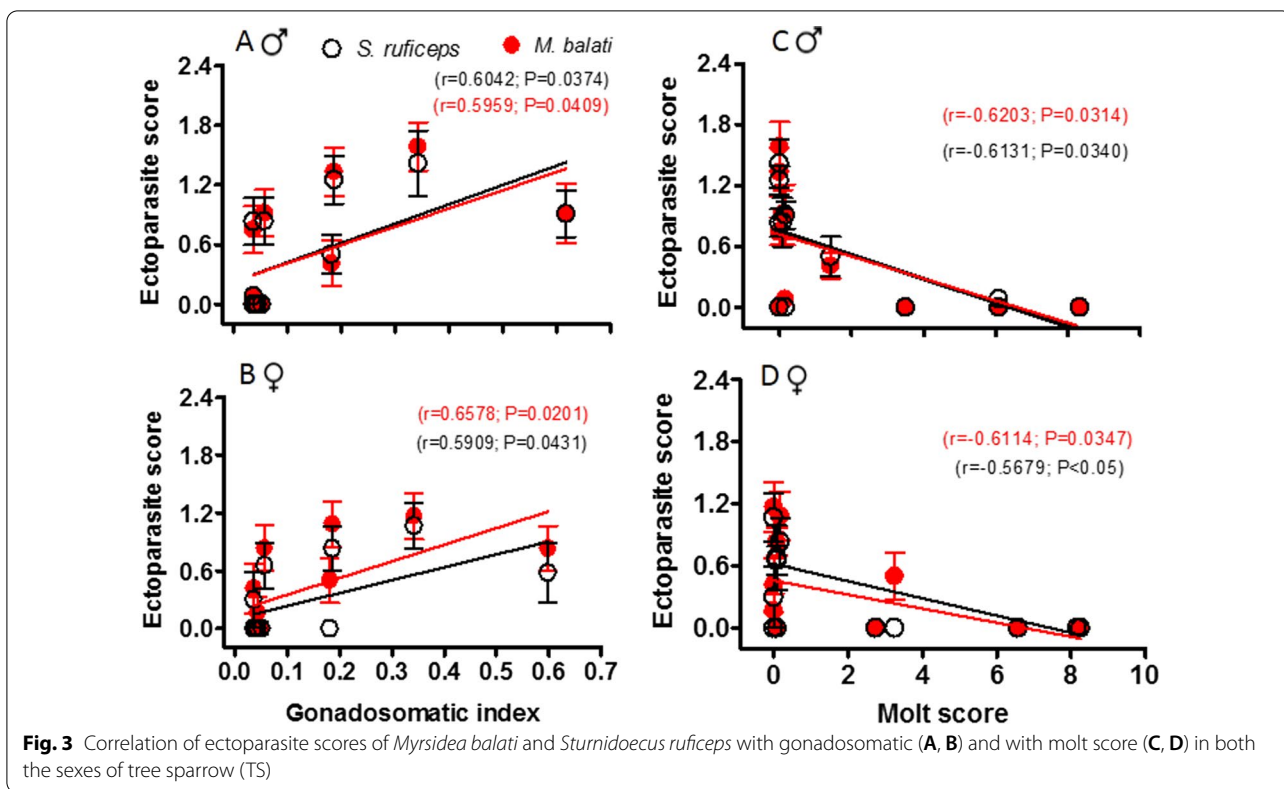


Fig. 2 Annual changes in gonadosomatic index and molt score (A), prevalence score (B) and infection percentage of *Myrsidea balati* and *Sturnidoecus ruficeps* (C) in both sexes of the tree sparrow (TS)



of different behavioral traits of the tree sparrows during their breeding period (Fig. 4B). There was a positive correlation ($r=0.9679$; $P<0.0001$) between the duration of display of behavioral traits and parasitic infection indicating that the tree sparrow spent more time displaying these behaviors during the period of peak lice infection (Fig. 4C). The birds did not show significant display of behavioral traits during the time of active molt, and no correlation was noticed between display time and the molt ($r=-0.2201$; $P=0.1740$).

Discussion

Our results clearly suggest that the tree sparrows possess definite seasonal cycles of reproduction and feathers molt showing an almost similar pattern in both sexes (Fig. 2A). They exhibited an increasing gonadosomatic index (GSI) during spring (March–April) that reached to peak in summer (May) and declined spontaneously thereafter in late summer (June) to a minimum in autumn (August) which was maintained throughout the winter (September–February). The peak GSI in males was significantly higher as compared to females. The increase in GSI indicated the attainment of active reproductive phase and sexual maturity in terms of gonadal development while its decline signaled the beginning of photorefractoriness in the tree sparrow (Dixit & Singh, 2011; Eligi et al., 2020; Fig. 2A). The decrease in GSI is usually accompanied by a decrease in plasma levels of gonadal steroids and ultimately the cease of reproductive activities (Upadhyay et al., 2018). However, feathers molt in sparrows proceeded with declining GSI and extended from June to November with a peak in August. This suggests that the two high energy involving life-history stages, i.e., reproduction and feathers molt in the tree sparrow, do not coincide and occur at different times. Similar to tree sparrow, majority of avian species save huge energy costs by molting immediately after breeding which enhances bird's survival value (Dixit & Singh, 2012, 2020). Further, the prevalence score and percentage of parasitic infections of both the lice species followed a cyclic pattern running parallel to the GSI and antiparallel to the feathers molt in both the sexes of tree sparrow. The above findings in tree sparrow are in conformity with the earlier reports on several lice species that synchronize their life-history stages with those of their host species (Altizer et al., 2004; Dietsch, 2005). A study on three species of woodpeckers (*Picoides pubescens*, *Sphyrapicus varius* and *Colaptes auratus*) showed that they had similar patterns of infestation by six species of lice. In all the three woodpeckers species, the lice infestations usually reduced from their respective spring time intensities to their lower most values during or at the end of the reproductive season of their hosts and then increased again in during the fall (Lamb & Galloway,

2016). In a different study on comparison of breeding cycles of the common myna (*Acridotheres tristis*) and the three louse species (*Menacanthus eurysternus*, *Brueelia* sp. and *Sturnidoecus bannoo*) infection, it was observed that egg index of the lice coincided with the breeding period of host bird (Srivastava et al., 2003). A distinct sex difference in the prevalence score and infection percentage of both the lice species infecting tree sparrow was noticed with more infection in male birds as compared to females (Fig. 2B–C). Similar to our above finding in tree sparrows, the infestations of *M. eurysternus* (hematophagous louse) were also found higher in males as compared to female birds. Further, the infection was still higher in case of non-hematophagous louse (*S. bannoo*) (Srivastava et al., 2003). It may be inferred from above findings on our study birds together with some other avian species that the reproductive hormones of the host birds control the timing of breeding of hematophagous lice species (Foster, 1969). The ectoparasite infestation was higher in males as compared to females particularly during breeding season when testosterone level was recorded higher. This suggests that the increase in plasma level of testosterone often exerts an immunosuppressive effect and impairs the ability of the male birds to deal with ectoparasites resulting in the high magnitude of infection during reproductive period in males when compared to female (Poiani et al., 2000; Saino et al., 1995). This is supported by a study on barn swallows (*Hirundo rustica*) which suggests that the implantation of testosterone leads to an increase in number of hematophagous lice (i.e., *Macharilaemus malleus* and *Myrsidea rustica*) (Saino et al., 1995). However, in light of the above facts and on the basis of our findings, we are not in a position to explain how the testicular hormones of the tree sparrow could affect the reproductive rate of non-hematophagous species like *S. ruficeps*. Further investigation is required to give a clear-cut explanation in this regard.

Although the infestations of both the parasites were found to be positively correlated with the GSI in both sexes of tree sparrow, they were negatively correlated with feathers molt (Fig. 3A–D). Molt, in both the sexes of sparrows, proceeded with the decrease in GSI and was accompanied with the significant decrease in ectoparasitic lice infections. Similar to our observation on tree sparrow, there are reports of an apparent decrease in ectoparasite load with the progression of the host's feather molt in some other avian species (Clayton et al., 2010). In a study on Eurasian blackbirds (*Turdus merula*), it was observed that there was 85 percent reduction in the abundance of lice during the period of molt (Baum, 1968). A decline in the population of ectoparasites was also observed on European starlings (*Sturnus vulgaris*) during the autumn month when they are in

their molting stages (Markov, 1940). Further, it has been reported that the occurrence of lice is lower on those birds that molt twice than those that molt only once a season as observed in sharp-tailed sparrows (*Ammodramus caudacutus*) when compared to seaside sparrows (*Ammodramus maritimus*) (Post & Enders, 1970). However, in contrast to our observation on the tree sparrow, the louse (*Menacanthus alaudae*) population on male house finches (*Carpodacus mexicanus*) was found to increase during the molting season. Further, molting males had more lice than molting females (Hamstra & Badyaev, 2009). A photoperiodic manipulation study that induced early feather molt in rock pigeons (*Columba livia*) indicated a reduction in louse abundance by visual examination method (Moyer et al., 2002). On the other hand, body washing method showed that the molt did not reduce the abundance of lice (Clayton & Drown, 2001). The difference in lice abundance between the two methods during the period of feathers molt may probably be due to the fact that lice are not easily observable during visual examination of the new lush plumage that masks the lice and also due to the fact that they shelter inside the sheaths of newly developing feathers. Studies using more robust methods for quantifying lice like fumigation of common mynas (*Acridotheres tristis*; Chandra et al., 1990) and body washing of house sparrows (*Passer domesticus*; McGroarty & Dobson, 1974) indicated a decrease in louse number in late summer that coincides with postnuptial molt. Thus, the role of feathers molt in controlling mobile parasites like lice is still inconclusive and needs further investigation.

Although there was a significant decrease in hematocrit % at the times of peak GSI and parasitic infection (female: April) and also feathers molt (male: July/August, and female: July) in both the sexes of tree sparrow, no correlation was observed between the ectoparasite infection and hematocrit % (Figs. 2A and 4A). Further, no sex difference was observed in the variations of hematocrit % in the tree sparrow. In wild birds, the hematocrit % has been commonly used as one of the indicators of the physiological condition like anemia (Ots et al., 1998; Saino et al., 1997). The established hematocrit % for caged birds ranges from 35–55. Less than < 35% is regarded as anemic (Campbell, 1994). Study on ectoparasites infection on chickens by Al-Saffar and Al-Mawla (2008) observed that there was a significant decrease in hematocrit % indicating anemia due to the blood sucking mite and ticks but not due to lice or flies which are non-blood sucking ectoparasites. The decrease in hematocrit % during the peak period of ectoparasite infection in tree sparrow might be due to the heavy infection of *M. balati* that feeds on feathers as well as blood. Although the hematocrit % decreased during the peak infection period in female sparrow, it (male:

36.93–44.16%; female: 36.5–41.83%) was found above the level of anemia. It has been documented in many species of birds that the females have reduced hematocrit % leading to anemia during their egg laying period (Gayathri & Hegde, 2006; Jones, 1983). Similarly, a decreased level of hematocrit % was also observed in the female tree sparrows during the period of peak ovarian development and time of ovulation. Possibly in female estrogen inhibits erythropoiesis (red blood cell synthesis) that lower the hematocrit %, while the male hormone androgen increases this process (Wagner et al., 2008). Tree sparrows showed a decrease in hematocrit % during peak molt period. The above response in tree sparrow is supported by the report that low hematocrit % may occur due to conditions caused by molting or migration (Young et al., 1993). Study on physiological stress induced by molt on African penguins, *Spheniscus demersus*, revealed decrease in the value of the hematocrit and red blood cells (Mazzaro et al., 2013). Though the host immune response plays a central role against the parasite infection, it comes with some costs. The host has to trade off the energy required for stimulating immune response with the other nutrient-requiring functions, i.e., sexual signalling, breeding performance and growth (Henson et al., 2012). Moreover, the immune system may be very effective even in defense against chewing lice that do not feed on blood (James, 1999).

The display time of various behavioral traits during the breeding period (January–May) with high GSI and parasitic infection was significantly higher ($P < 0.05$) than the time during non-breeding period (June–December) with low GSI and parasitic infection in the tree sparrow (Figs. 2A–C and 4B). Further, there was increase followed by decrease in the duration of display of behavioral traits in the tree sparrow with maximum duration during the breeding period (Fig. 4B). Further, there was a positive correlation ($r = 0.9679$; $P < 0.0001$) between display duration of behavioral traits and parasitic infection indicating that the tree sparrows spend more time in showing these behaviors during the period of peak lice infection (Fig. 4C). However, the birds did not show significant behavioral traits during the time of active molt. The above findings on the tree sparrow clearly suggest that the duration of display of behavioral traits in them may have a major impact on lice occurrence. The avian species that cannot efficiently groom usually experience enormous rise in the number of lice (Clayton et al., 2010; Moyer et al., 2002). The birds with more species of lice devote more time in preening than those of the birds with less species of lice (Cotgreave & Clayton, 1994). In a study on poultry, the grooming rate was found to increase in heavily infested amblyceran lice (Brown, 1974). Similar observations

were recorded in our study birds that spent more time in display behavior during the peak period of lice infection. According to Rothschild and Clay (1952), bathing and dusting followed by grooming aid birds to get rid of parasites. Bird exposure to solar radiation is called sunning and is thought to kill lice directly or by increasing their susceptibility to grooming as they attempt to escape from the heat (Moyer & Gardiner, 1995). However, the energy and time necessary for effective display of behavioral traits to control lice might also be costly. For example, birds that spend more time on grooming will have very less time available for other activities such as finding mates, foraging and territorial protection. It may also reduce vigilance increasing the chances of being killed by predators (Redpath, 1988).

Ectoparasite infestation has direct consequences on the fitness of the birds. The immunological suppression by testosterone most likely increases greater vulnerability to parasitic load during the reproductive season. Accordingly, any suppression of immune functions may impair future reproductive performance (Hanssen et al., 2004). A long-term study of 4 years involving manipulation of infection on great tits (*Parus major*) by hen flea (*Ceratophyllus gallinae*) resulted in lower reproductive performance. Females lay considerably fewer eggs, and the nestling period was extended (Fitze et al., 2004). It increases host mortality rates and decreases the lifespan of the birds. In a different study on cliff swallow (*Hirundo pyrrhonota*) infected with the ectoparasite load of cimicid bugs, fleas and chewing lice resulted in decrease in survival and the host losing up to 1 year of reproductive success (Brown, et al., 1995). Ectoparasite infestation also affects mate selection in birds. In a study on parasite mediated sexual selection, lice infected male Rock Doves failed to mate as the female Rock Doves selected louse-free males, presumably based on a modified secondary sexual characteristic and male display (Clayton, 1990).

Conclusions

Thus, we can conclude that the tree sparrows adopt various adaptive strategies like feathers molt and display of various behavioral traits during breeding and non-breeding periods to control their parasitic load and also to avoid energy conflict with other high energy demanding processes like reproduction and molt.

Abbreviations

BW: Body weight; GSI: Gonadosomatic index; GW: Gonadal weight; IB: Infected birds; SEM: Standard error of mean; PI: Percentage of infection.

Acknowledgements

The permission for the capture of birds from the Department of Environment and Forest, Government of Meghalaya, Meghalaya, is greatly acknowledged.

Author contributions

ASD conceived the idea, NSS and DK performed the experiments, and ASD and NSS wrote the manuscript. All the authors read and approved the manuscript.

Funding

Not applicable.

Availability of data and materials

This published paper contains all of the data collected throughout the research.

Declarations

Ethics approval and consent to participate

All the experiments and animal care were carried out under the guidelines of the institutional animal ethics committee of the North-Eastern Hill University, Shillong, India (1886 of 04. 12. 2014).

Consent for publication

Not applicable.

Competing interests

All the authors declare that there is no conflict of interest.

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Received: 1 September 2021 Accepted: 27 November 2022

Published online: 05 December 2022

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