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TRICHOBILHARZIA SPP. EGG PRODUCTION IN COMMON MERGANSER (*MERGUS MERGANSER*) DUCKLINGS, SECOND-YEAR ADULTS, AND BROODING HENS IN NORTHERN MICHIGAN

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Miracidia

ABSTRACT

Swimmer's itch is caused by the accidental penetration of human skin by various species of avian schistosomes that naturally cycle in bird and snail hosts. Little is known about the ontogeny of avian schistosomes in their vertebrate hosts, especially in wild birds. Taking advantage of the abundance of common merganser (*Mergus merganser*) broods on northern Lower-Peninsula lakes in Michigan, we obtained fecal samples from 97 common mergansers, focusing on ducklings (n = 75) of 13 different ages but also including birds that were 1 yr and older. Miracidia hatching from fecal samples were quantified per gram of feces to determine the timeline and reproductive output of naturally acquired schistosome infections. All ducklings 18 days or younger were negative. Beginning at 21 days old, some ducklings were passing a small number of eggs, with the percentage of ducklings passing eggs increasing with age. The number of eggs passed by ducklings remained low until approximately 7 wk of age. At 52 days and older, all ducklings were passing eggs and the number of miracidia produced was frequently many times higher, strongly consistent with published mitigation studies that duckling relocation severely reduces snail infections and case reports of swimmer's itch. Surprisingly, second-year common mergansers also passed high numbers of schistosome eggs but may contribute less to successful transmission to snails on the basis of the published success of mitigation by duckling relocation. All brooding hens sampled were positive but passed low numbers of eggs. This is the first study of the development patterns of any avian schistosome in wild young-of-the-year birds, and the patterns are compared with the few known laboratory studies on worm development.

Avian schistosomes are a diverse, cosmopolitan group and their cercariae are the primary cause of swimmer's itch or cercarial dermatitis. The northern third of the Michigan Lower Peninsula has a rich history regarding the study of avian schistosomes, as it was at the University of Michigan Biological Station on Douglas Lake that the link between avian schistosomes and swimmer's itch was first made (Cort, 1928). Numerous studies of avian schistosomes through the decades since have been based in northern Michigan and continue almost 100 yr later.

One of the first avian schistosome species observed in northern Michigan was initially described from cercariae emerging from *Stagnicola emarginata* and temporarily named *Cercaria stagnicolae* (Talbot, 1936). This species was frequently noted as the most common cause of swimmer's itch in northern Michigan (Cort, 1936, 1950; Cort et al., 1937, 1940) and in Wisconsin, Minnesota, and Manitoba (McMullen and Brackett, 1941) in part because of the abundance and habitat preferences of its snail host (sandy substrates that humans also find attractive for swimming). McMullen and Beaver (1945) succeeded in obtaining adult worms from two experimentally infected canaries and formally described the species as *Trichobilharzia stagnicolae*. A natural host for *T. stagnicolae* was not known until Blankespoor and Reimink (1991) used miracidia from the feces of hatch-year common mergansers (*Mergus merganser*) from Glen Lake to infect *S. emarginata* snails and produce cercariae that matched the original description (Talbot, 1936). Molecular methods have confirmed that common mergansers are host to both *T. stagnicolae* and *Trichobilharzia physellae* (Brant and Loker, 2009) and when surveyed, common mergansers are infected with schistosomes at high rates in northern Michigan (Blankespoor and Reimink,

1991; Blankespoor et al., 2001) and elsewhere (Loken et al., 1995; Leighton et al., 2000). *Trichobilharzia stagnicolae* remains a dominant schistosome (by abundance) in northern Michigan (Keas and Blankespoor, 1997; Coady et al., 2006; Rudko et al., 2019; Soper et al., 2023; Blankespoor et al., 2024) and it has a much higher propensity to penetrate human skin than another recently described but common schistosome in northern Michigan (Anderson et al., 2022). The frequency and severity of swimmer's itch induced by *T. stagnicolae* and the economic impacts on some northern Michigan lakes have led to substantial attempts to mitigate the problem (Blankespoor and Reimink, 1991; Rudko et al., 2022; Blankespoor et al., 2024).

Relatively little is known about the development time of *T. stagnicolae* in the vertebrate host, especially in wild birds. In experimental canary infections, examination by necropsy took place 47–48 days after exposure and by that time mature worms were present and producing eggs (McMullen and Beaver, 1945). We investigated the time to maturity of *T. stagnicolae* in wild populations of the only known definitive hosts, relying on the abundance of hatch-year common mergansers at 4 northern Michigan lakes and that their infections must have been acquired on the lake sometime between their first day after hatch and the time of sampling. The 4 lakes were Burt Lake (Cheboygan County), Crystal Lake (Benzie County), Glen Lake (Leelanau County), and Higgins Lake (Roscommon County). On all 4 lakes, *S. emarginata* is the dominant snail by abundance and *T. stagnicolae* is the dominant schistosome by abundance on the basis of all measures available (Blankespoor and Reimink, 1991; Saxton, 2001; Coady et al., 2006; Rudko et al., 2019, 2022; Soper et al., 2023; Blankespoor et al., 2024), though *T. physellae* and its snail hosts (*Physella* spp.) are present in lower abundances. More important, none of these lakes was participating in any swimmer's itch control measures in the summers before the sampling in this study (2022 and 2023), and all had numerous cases of swimmer's itch in the years of sampling (2023 and 2024).

In June–August of 2023 and 2024 we obtained fecal samples from 97 individual birds, including 75 ducklings of 13 different ages, 16 second-year birds (females in their second summer spend this time prospecting for future nests and do not breed until their third summer; Pearce et al., 2020), and 6 brooding hens. Fecal samples were obtained either by trapping broods and holding them for a short time in pet cages before releasing them (ducklings and hens in separate cages) or after directly observing individual birds defecate on docks or other structures. Duckling ages were primarily determined by plumage development to within ± 2 days (Erskine, 1971; Pearce et al., 2020). In addition, lake residents could also report the appearance of broods via electronic submission. The date of the first appearance provided a minimum age for specific broods and often could be used to corroborate ages determined by plumage. Sample sizes from each lake were: ducklings, $n = 51$ from Crystal, 15 from Burt, and 9 from Higgins; second-years, 10 from Burt, 3 from Crystal, 2 from Glen, and 1 from Higgins; and hens, 3 from Crystal, 2 from Higgins and 1 from Burt. Every sample represents a unique individual at a given time point and all individuals were sampled only once during the study.

Fecal samples were collected using flexible forceps to transfer feces (avoiding the uric acid) to a 35-mm petri dish containing moistened filter paper (to prevent sample drying), labeled, and kept on ice or in a refrigerator for a maximum of 36 hr until analysis. In the laboratory, samples were weighed to the nearest 0.01 g and transferred to a 100-mm glass petri dish. The average sample mass was 0.29 g for ducklings, 0.48 g for second-year birds, and 0.69 g for hens (samples greater than 1.0 g were split between 2 dishes). Each sample was then homogenized in the petri dish using well water or artificial pond water (Collins et al., 2024) and clean forceps, allowed to settle for 30 sec, and then a portion of the water was decanted to remove nonsettling material. Addition and decantation of water occurred an additional 1–3 times until the sample was relatively clear. Samples were then left exposed to light for at least 75 min (Guth et al., 1979). Schistosomes are relatively unique in that the eggs are fully embryonated and miracidia can hatch from eggs within minutes, whereas most other parasite eggs, even closely related trematodes, require days or weeks of embryonation and are not likely to hatch and be motile in the water in such a short time frame (Roberts and Janovy, 1996).

Each sample was examined by a light microscope to determine the presence of schistosome miracidia. Egg production was quantified by counting the number of miracidia over 4 (1-min) intervals. To prevent double counting, miracidia were removed by pipette as they were observed. This method results in counting all or nearly all the miracidia present in most samples and although samples with heavy infections had some uncounted miracidia remaining, this was minimal. Fourth-minute interval counts always resulted in 0 or a lower number of miracidia observed than in the previous intervals, so all miracidia were counted in all but the heaviest infections with a substantial amount of fecal material. The total number of miracidia counted was used to calculate the number of miracidia per gram of feces. Samples that were negative after 4 intervals were observed for an additional 2 min to ensure that they were negative, with no samples changing status from negative to positive. For a subset of samples from ducklings ($n = 26$, Burt Lake, Crystal Lake, Higgins Lake), a small number of miracidia (3–30) was preserved for species identification by species-specific quantitative polymerase chain reaction (Rudko et al., 2019). As expected, all samples were positive for *T. stagnicolae*, and 5 duckling samples were also positive for *T. physellae* (all 5 from Crystal Lake). Thus, the findings we describe here largely reflect the biology of *T. stagnicolae*, but also of *T. physellae*. The miracidia of the 2 species are not easily distinguished and so could not be counted separately.

Miracidia counts show some expected patterns in ducklings. First, young ducklings were not passing schistosome eggs, with all samples ($n = 28$) negative at 12, 15, 17, and 18 days old (Fig. 1). Positive samples were first detected at 21 days old (1 of 3 ducklings) and the percentage of positive samples generally increased with duckling age (Fig. 1), although there was at least 1 duckling negative at 26, 28, 35, 42, and 50 days ($n = 32$; Fig. 1). It is likely that ducklings steadily acquire worms as they age but the occurrence of individuals that test negative may reflect individual host characteristics, the time that may be required for these dioecious worms to find a mate inside their host, or just the stochasticity expected among samples with lower overall counts of miracidia. Indeed, Rau et al. (1975) reported high variability among hourly collections of laboratory-infected ducks. F1

At older ages (52, 61, and 65 days; $n = 15$) all duckling samples were positive and many had high miracidial counts, multiple times higher than younger ducklings and brooding hens (Fig. 2). We note that it is not possible with our data to determine a F2

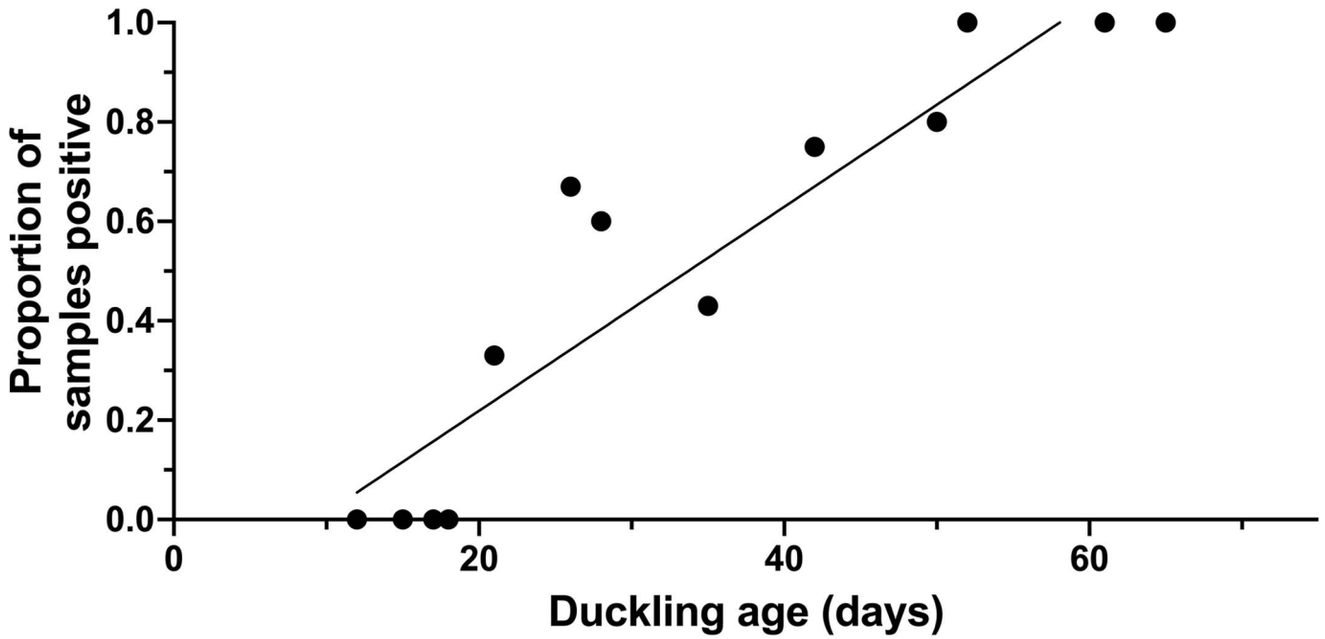

Figure 1. Proportion of fecal samples positive for *Trichobilharzia* spp. miracidia from common merganser (*Mergus merganser*) ducklings (n = 75) of 13 different ages. Each black circle represents an age group.

definitive date at which elevated egg production can be detected, but speculate that it could occur earlier, depending on the rate at which ducklings encounter cercariae in the first few weeks of life. High miracidial counts were expected in older ducklings as they had been an ample source of miracidia in elucidating the life cycle of *T. stagnicolae* (Blankespoor and Reimink, 1991). This observation, that common merganser ducklings were important for elevating the population of *T. stagnicolae* on northern Michigan lakes, formed the basis of a successful lake-wide reduction of this schistosome on Glen Lake in the 1980s (Blankespoor and Reimink 1991). In more recent years, we implemented a strategy of brood relocation at Higgins Lake and Crystal Lake, with >98% and >90% reductions, respectively, of the *T. stagnicolae* population in *Stagnicola* snail hosts and a correspondingly dramatic reduction in swimmer's itch cases (Blankespoor et al., 2024). Such an effect strongly demonstrates the important role of ducklings vs. migrating birds that are present in large numbers in the spring and fall seasons. Surprisingly, another group attempted the same mitigation method at Glen Lake in the same time frame and contended that it was not effective (Rudko et al., 2022); however, differences between these 2 mitigation studies and their assessment methods are discussed in Blankespoor et al. (2024).

Consideration of the egg production seen in older ducklings in this study highlights just how many miracidia they can deposit in a day: at a value of 50 miracidia per gram (mid-range value in our data), even a low estimate of 1 g of feces released per hour results in 1,200 miracidia released per duckling per day. In laboratory infections, Rau et al. (1975) recorded daily miracidia counts of up to 20,717 per individual for *Trichobilharzia szidati* in black ducks (*Anas rubripes*). Certainly, large percentages of these miracidia do not succeed because they get eaten, die before encountering a snail, penetrate the wrong snail species, or fail to fully develop in the correct snail species (Loker et al., 2022), yet the reproductive potential for the parasite is very evident. In our data, the earliest elevated egg production was at 52 days (Fig. 2), but it seems possible it could occur earlier if the snail infection level is high and ducklings are encountering cercariae frequently. It should also be noted that large numbers of miracidia entering the water are a potential source of environmental DNA (eDNA) because once the miracidia die, a portion of them is likely to release DNA into the environment (becoming cell-free eDNA). Continuous deposition of miracidial eDNA into the water could affect recent methods that rely on DNA copy numbers to estimate numbers of live cercariae, especially when the assumption is made that all eDNA detected is from live cercariae and dead cercariae and miracidia are disregarded as eDNA sources. Such methods have been used to assess swimmer's itch risk (e.g., Rudko et al., 2018, 2019, 2020) and to assess the effects of swimmer's itch mitigation (Rudko et al., 2022).

We were surprised to find that second-year common mergansers sampled often had high miracidial counts (Fig. 2) because mitigation of swimmer's itch at Crystal Lake and Higgins Lake was so effective despite the consistent presence of second-year common mergansers on these lakes during the summer brooding season (Blankespoor et al., 2024). Of interest, a close look at the data in the present study revealed that of the 16 second-year samples, the 7 highest miracidia counts were collected between June 19 and July 1, whereas the 7 lowest miracidia counts (including the only 3 that were negative) were in those samples collected between July 13 and July 24. Perhaps schistosome egg passage in second-year birds is elevated for a time after migration and then subsides, lessening their impact, but more data are needed to see if this pattern holds, ideally by sampling the same birds multiple times over this period. Additionally, it is possible that the viability and infectivity of miracidia may be maximal in those from ducklings but is diminished in second-year birds because of the

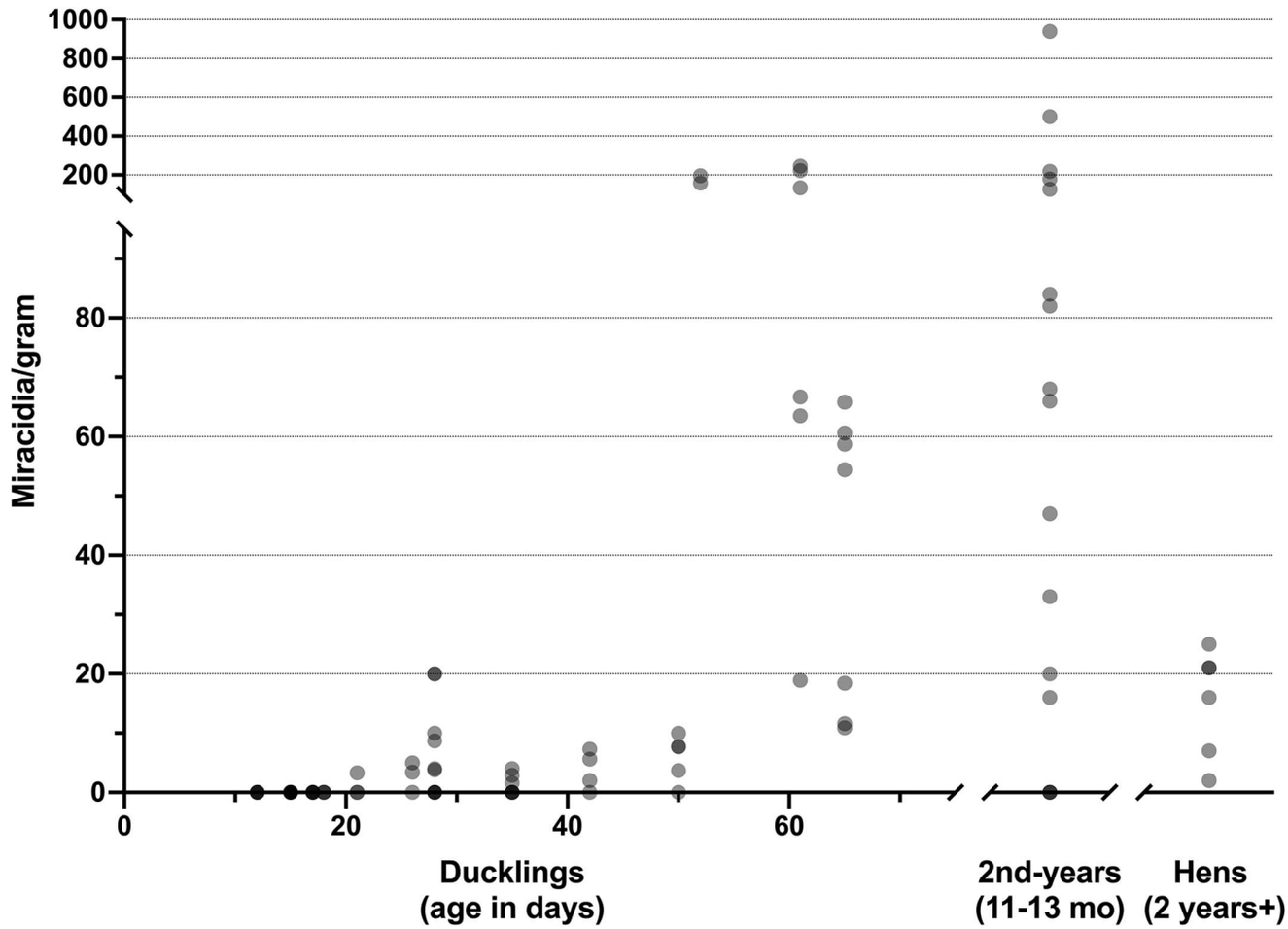

Figure 2. Number of miracidia per gram in fecal samples from common merganser (*Mergus merganser*) ducklings (n = 75), second-year individuals (n = 16), and brooding hens (n = 6). Each gray circle represents 1 individual, with overlaps producing darker grays.

host immune system maturation or exposure to more worms. It has been reported that in the laboratory, *T. szidati* egg production peaks in Pekin ducks (domestic mallard, *Anas platyrhynchous*) at 15–22 days postexposure, then declines rapidly to near zero by 30 days postexposure, and, of interest, so does miracidial infectivity (Meuleman et al., 1983). A compelling experiment would be to compare the infectivity of miracidia from wild ducklings with that of miracidia from second-year or other adult birds.

Although our sample size of brooding hens was not large (n = 6), miracidia counts were low and consistent with semiquantitative observations we have conducted in the past (personal observations). Therefore, despite spending as much time in the water as their broods, brooding hens may be less important to summertime transmission to snails. However, they are a host that has survived into reproductive adulthood, including multiple migrations, offering an effective dispersal vehicle to the parasite. Whether egg production is similar in other adult hosts such as breeding males and migrating or wintering common mergansers is not known, and we did not have the opportunity to sample them.

To our knowledge, this is the first study to assess the development of avian schistosomes in wild ducklings, so comparisons with our data are limited to surveys of wild birds and a small number of laboratory studies. The high prevalences reported here in ducklings older than 50 days (100%, n = 15), brooding hens (100%, n = 6), and second-year birds (81.3%, n = 16) are consistent with the high prevalences found in all of the surveys of common mergansers mentioned previously (89%, n = 27, Blankespoor and Reimink, 1991; 83.9%, n = 87, Loken et al., 1995; 81.7%, n = 120; Leighton et al., 2000; 100%, n = 51, Blankespoor et al., 2001). Few other data on schistosome prevalence in mergansers are found in the literature: in Europe, KoláŘová et al. (2013) found 14 of 19 (73.6%) red-breasted mergansers (*Mergus serrator*) infected; Jouet et al. (2010) found 1 of 1 common merganser infected; Skirnisson and KoláŘová (2008) found 5 of 6 red-breasted mergansers infected; and in North America Brant and Loker (2009) found 3 of 6 common mergansers and 0 of 3 red-breasted mergansers infected.

Laboratory and life-cycle studies of avian schistosomes have indicated that infections are short-lived and that the period of egg production is short, on the order of only 2–3 wk, with all worms disappearing from the intestine and most dying (Bourns et al., 1973; Rau et al., 1975; Meuleman et al., 1983; Horák et al., 2002), although a small number of *T. szidati* worms were observed in the

livers of black ducks well after the patent period (Bourns et al., 1973). The brevity of infections and egg passage combined with the observation that infection success and worm development are usually severely reduced in challenge (second or third) infections (Ellis et al., 1975; Rau et al., 1975) makes it difficult to explain how wild birds, including adults, are so commonly found to be releasing eggs, in some cases in large numbers. One feature of the laboratory studies is that almost all involved single exposures to very large numbers of cercariae (hundreds up to 15,000), which is unlikely to represent the rate at which birds encounter cercariae in nature. However, even after more realistic consecutive daily exposures to small numbers of cercariae (e.g., 25), infection success and egg production of subsequent challenge exposures were severely reduced (Rau et al., 1975), which suggests that wild birds are likely to acquire at least some immunologically based resistance to infection or egg production. Further complicating matters, challenge exposures also appeared to induce brief egg laying and release by the few worms that remained from the initial infection after the patent period (Rau et al., 1975). In addition, factors such as stress from migration and the genetic diversity of schistosomes encountered could affect susceptibility to infection and avian schistosome egg output. Hence, the natural dynamics and duration of infection of avian schistosomes in their vertebrate hosts remain poorly understood. Given the difficulty of conducting laboratory and life-cycle studies like those mentioned above, as well as restrictions that may come from animal use considerations, future insights seem most likely to come through study of wild birds as presented here. Time-series sampling of individual wild birds or of broods would be of especially high value.

The authors assert that all applicable national, state, and institutional guidelines for the care and use of animals in research were followed. All sampling, trapping, and banding activities by the authors were conducted with permission from the U.S. Fish and Wildlife Service (Scientific Collecting permit MB54823B), the U.S. Geological Survey (Bird Banding Master permit 24094), and the Michigan Department of Natural Resources (Scientific Collecting permit SC1543). All protocols involving animals were reviewed and approved by the Calvin University Institutional Animal Care and Use Committee (BR2023-01 and BR2024-02). Funding was provided by the Higgins Lake Swimmer's Itch Organization.

Conflict of interest: The authors operate a company that provides scientifically based swimmer's itch assessment and mitigation services. There are no other conflicts of interest.

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AUTHOR QUERIES

AUTHOR PLEASE ANSWER ALL QUERIES 1

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