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Female-biased sex ratio in a protandrous moth: challenging the mate opportunity hypothesis for explaining protandry

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Asynchrony among sexes in arrival/emergence timings is common in animals with distinct breeding periods. Scramble competition among males for virgin females is generally attributed to select for protandry among monandrous mating systems, especially in insects. This is classified as the 'mate opportunity hypothesis', or sexual selection for early male emergence. Sex ratio can influence reproductive asynchrony, and protandry is known to be favoured when sex ratio is male-biased. However, in the present communication, empirical evidence demonstrates female-biased pre-adult, adult and operational sex ratios in the monandrous, protandrous moth *Opisina arenosella*. It appears that males of *Opisina* need not compete among themselves for virgin mates, and that, males, irrespective of the time of emergence, have sufficient mating opportunities. These throw serious questions at the sexual selection theory for explaining protandry in *Opisina*. Additionally, data proved that the last arriving females died as virgins, which support models that predict loss of mating opportunities for females due to protandry.

Keywords: Mate opportunity hypothesis, mateless females, *Opisina arenosella*, protandry, reproductive asynchrony, sexual selection.

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IN animals with distinct breeding periods, often males and females do not synchronize their arrival/emergence timings. A situation where the mean arrival/emergence date for males is earlier to that of females is called 'protandry'. There are seven hypotheses to explain conditions leading to protandry in animals¹. They are, 'rank advantage hypothesis', where territorial males arrive early to capture the most favoured 'breeding sites'; 'mate choice hypothesis', where females assess their mates, therefore early arriving males have an advantage; 'susceptibility hypothesis', where females avoid an adverse early season, especially in seasonal climates; 'waiting cost hypothesis', where females have to wait for males to be ready and therefore delayed arrival helps in reducing death due to predation; 'outbreeding hypothesis', where differences in developmental durations of males and females could increase the probability of outbreeding, especially among populations at low densities; 'constraint hypothesis', where a trait correlated with early arrival of males (or delayed arrival of females) is strongly selected, and 'mate opportunity hypothesis', where males maximize their mating opportunities by emerging early, especially in monandrous insects (monandry refers to single mating in females).

Opisina arenosella (Walker) (Lepidoptera: Oecophoridae) (hereafter just *Opisina*) is a protandrous moth² that defoliates coconut palms in India and Sri Lanka. Remarkably, the species breeds throughout the year (aseasonal) with nearly five discrete generations^{3,4}. Protandry has been reported only among insects that exhibit marked seasonality; therefore the above hypotheses, while referring to insects, identify with seasonal species. However, as *Opisina* is aseasonal, it becomes interesting to understand the underlying factor(s) that drives protandry in this species. Females of *Opisina* are monandrous⁵, and populations are often large enough to cause extensive losses to coconut growers. Both sexes have been observed to mate on the night of emergence⁶.

For explaining protandry in *Opisina*, rank advantage and mate choice hypotheses can be ruled out, as males do not exhibit territoriality and females do not assess males (pers. obs.). The feature of aseasonality^{3,4} in *Opisina* discards susceptibility hypothesis. Since males and females mate on the night of emergence⁶, the waiting cost hypothesis can also be discounted. The high population densities of *Opisina* do not justify the outbreeding hypothesis as an explanation for protandry. The constraint hypothesis might also not explain protandry in *Opisina*, especially from the context of selection for body size⁷. Here, if males are selected to be smaller (or females larger), but develop at the same rate as females, they must develop early. Such a situation may be favoured in seasonal species where time and availability of food exert strong limitations on developmental duration⁸. However, such limitations do not exist in *Opisina*, as the species is aseasonal and its food, leaves of the coconut palm, is a peren-

nial resource. In addition, as selection for body size is easily achievable through difference in developmental rates, sexes need not compromise on reproductive asynchrony because theoretical studies suggest possible death of virgin females during protandrous emergence^{9,10}. The characteristics of monandry, high population density and discrete generations strongly support the mate opportunity hypothesis^{8,9} as an explanation for protandry in *Opisina*². Here, since females are monandrous and males polygynous (mate with several females), males that emerge earlier to females have the greatest opportunity to get virgin mates. The advantages of protandry can be realized only when generations are discrete⁸ and population densities are sufficiently high⁹. Under this hypothesis, owing to competition among males, protandry is favoured when the adult sex ratio is male biased⁹⁻¹¹ (and protogyny when female biased^{11,12}). On the contrary, certain observations have indicated that *Opisina* might have female-biased adult sex ratios^{2,6}. If true, it would put the mate opportunity hypothesis under the scanner, because, in that case, early emerging males would have little advantage over other males. However, due to monandry and polygyny^{5,6}, the operational sex ratios (OSR = males and females available for mating at a given time) could be male biased, which will still be able to explain protandry through the mate opportunity hypothesis. In this communication, we present results on pre-adult, adult and operational sex ratios in populations of *Opisina* before discussing the suitability of the mate opportunity hypothesis as an explanation for protandry in this species.

Adult sex ratio (number of male per female) was determined for three spatially segregated populations (refer Table 1, A, B and C for relevant details), which were thoroughly monitored through fortnightly sampling. A sample was drawn from each of the populations at the beginning of their respective flight periods (the period in a generation when adults are active) during one of the generations. During each sampling, damaged leaflets containing individuals of *Opisina* were collected at random from different palms, bulked and brought to the laboratory to separate out the caterpillars. Larvae (in their late instars) found in the samples were reared in the laboratory on coconut leaflets until pupation. Sexes were separated at the pupal stage and kept in containers for emergence of moths. The number of male and female moths that emerged was noted.

Male larvae have shorter developmental time^{2,13}; therefore, male larval mortality might be lower than that of females. However, due to early pupation, male pupae could face bulk of the initial onslaught by pupal parasitoids. Such factors could vary adult sex ratios depending on the extent of mortality inflicted by different agents. Therefore, pre-adult sex ratio of the population (at the pupal stage) was separately determined at another location by sampling pupal cases at the end of the flight period of a particular generation (Table 1, D). Ten palms

Table 1. Details of the infested orchards in south interior Karnataka, involved in the study

Location	Age of the palms (years)	Size of the orchard (palms)	Purpose of the study
A K. B. Doddi, Channapatna	20	600	Determining adult sex ratio
B Kuppala, Kadur	20–24	500	Determining adult sex ratio
C Mudugere, Channapatna	18–20	150	Determining adult sex ratio
D Kuppala, Kadur	20–24	500	Determining pre-adult sex ratio
E K. B. Doddi, Channapatna	20	600	Monitoring activity of moths through light traps and determining OSR

were selected at random from an infested garden, and three infested fronds were sampled from each. All the pupal cases present in the sampled fronds were brought to the laboratory and their sex ratio was determined. Chi-square test was applied to test if the observed sex ratio deviated from 1.

Adult sex ratio in all the three populations was female biased (Location A: 205 males, 461 females, sex ratio 0.44, chi-square = 98.40, $P < 0.01$; Location B: 145 males, 227 females, sex ratio 0.64, chi-square = 18.08, $P < 0.01$; Location C: 186 males, 283 females, sex ratio 0.66, chi-square = 20.06, $P < 0.01$). The pre-adult sex ratio was 0.64 (2008 males, 3150 females, chi-square = 252.84, $P < 0.01$).

These results show that the adult sex ratios vary between ~0.4 and ~0.6 males per female. As a male can mate with 3 or 4 females in its lifetime⁶, it appears that the sex ratio may be sufficient to ensure that all females mate. Nevertheless, this would be true only if this ratio is constantly maintained during each night of the flight period. But, as *Opisina* is protandrous, the sex ratio is male biased during the initial few nights of the flight period and later becomes increasingly female biased². This should obviously result in variable number of mating opportunities along the flight period. Therefore, it becomes necessary to resolve the OSR during each night to envision mating opportunities available to the sexes.

The OSR was determined for the moths sampled through three light traps set up during the flight period of a generation (Table 1, E; this study is a part of the investigations made to determine the daily abundance pattern of male and female moths within a flight period; the methodological details have been provided elsewhere²). As female *Opisina* begins to oviposit one night after the night of mating^{3,6}, each 'gravid' female (a female was considered 'gravid' when the ovaries, on dissection, revealed that eggs were not laid) caught on a particular night can be assumed to have been available for mating on that night. As males are polygynous and mate once in a night⁶, all active males were considered as available for mating once during a night. However, considering that males, on an average, mate with 3 or 4 females in a lifetime of ~8 days^{2,6}, it appears that mating opportunities for males are being overestimated. Correcting this overestimation is complicated, as a male may not mate on any of the nights

in his life⁶. Moreover, allowing this overestimation does not seem to influence our main inference (discussed later in this communication). Therefore, OSR was determined as the ratio of the number of males trapped in the light trap to the number of gravid females trapped in the light trap on each night of the flight period. Deviation of the OSR from 1 : 1 was tested through chi-square test.

The overall OSR differed significantly from 1 (OSR = 0.50; 2130 males; 4246 gravid females; chi-square = 702.24; $P < 0.00$) with a strong female bias. The OSR was >1 (2.79 males per gravid female) only during the initial 10 nights, which is prior to the peak flight period (11th to 19th night, Figure 1). During the peak flight period, the OSR was female biased (OSR = 0.45, 1405 males, 3137 gravid females, chi-square = 660.46, $P < 0.00$).

Interestingly, although *Opisina* is protandrous², we discovered the pre-adult (pupal), adult and OSR of the population to be female biased (OSR is female biased in spite of an apparent overestimation of mating opportunities for males). The OSR, which was initially male biased, became female biased even before 10% of the total moths appeared and it remained so till the end of the flight period (Figure 1), thus questioning the possibility of male-male competition for virgin females. If the mate opportunity hypothesis was to be supported, then, scramble competition among males for virgin females was expected on each night of the flight period, i.e. OSR would be male biased on each night of the flight period. In *Opisina*, as males are capable of mating on the night of emergence, and mate with not more than one female per night⁶, there might be no scramble competition among males for virgin females. Here, early emerging males might have no greater mating advantage than synchronously emerging ones. This is not in favour of the existing mate opportunity hypothesis¹; males of *Opisina* emerging throughout the flight period had sufficient mating opportunities.

In fact, the literature shows that protandrous taxa are often male biased (butterfly, *Euphydryas editha*^{14,15}; grasshopper, *Sphenarium purpurascens*¹⁶; bumble bees¹⁷; pacific salmon, *Oncorhynchus* sp.¹⁸; frog, *Rana dalmatina*¹⁹; migratory birds (mentioned in Kokko *et al.*¹¹); also in the lizard, *Anolis carolinensis*²⁰); but not in the case of Richardson's ground squirrels, *Spermophilus richardsonii*, where the adult sex ratio is female biased (<http://>

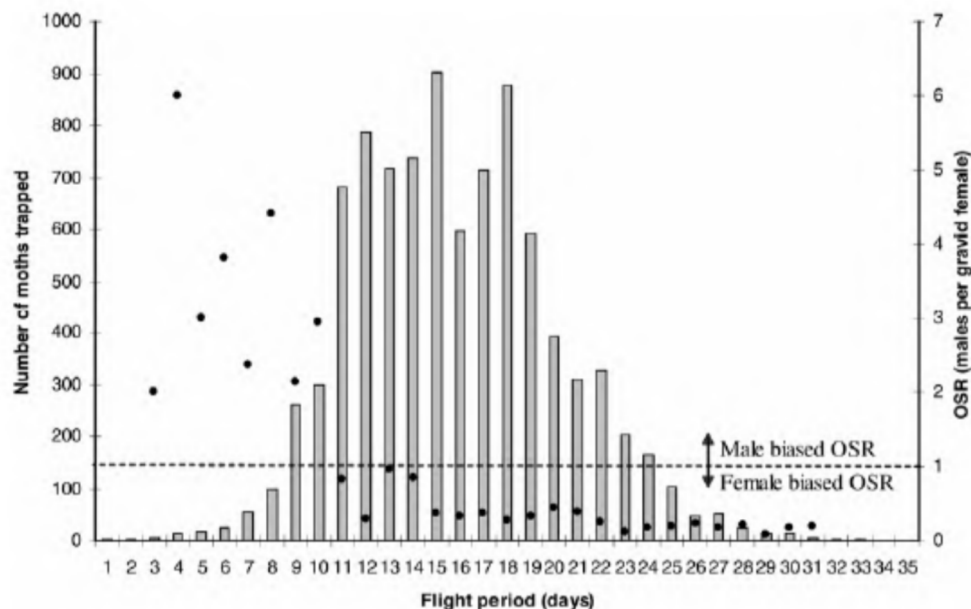


Figure 1. Number of moths sampled (columns) and the operational sex ratio (OSR) (dots) on each night of the flight period. (Moths have been sampled from three light traps run throughout the flight period of one of the generations. Sexes have been separated on each night and data recorded. Females were dissected to find out their ovarian condition (further details can be obtained from ref. 2).) Points above and below the horizontal dotted line show male- and female-biased OSR respectively. Only males were trapped during the first two nights, and no males were trapped during the last four nights of the flight period. Adult sex ratio became female biased from the 11th night till the end of the flight period².

people.uleth.ca/~michener/main.htm). Protandry is quite common across Class Insecta²¹. Among protandrous arthropods, the sponge-associated temperate water mite, *Unionicola crassipes* has been reported to have female-biased sex ratio²². The same report²² states that protandry may be a consequence of selection for smaller male body size (when sexes have similar growth rates, shorter development time for males would result in protandry and smaller body size), not for providing any mating advantage for males. In the UK, the sycamore aphid, *Drepanosiphum platanoidis* displays protandry when population densities are high, and it is suspected to have female-biased operational sex ratios²³. However, there are no reports explaining the relation between the sex ratio of the aphid and protandry. In an interesting situation, the protandrous butterflies, *Pieris napi*, *Polygonia c-album* and *Pararge aegeria*, which in a year, undergo a partial second generation (in strictly seasonal environments these butterflies complete a generation directly without undergoing any diapause while the succeeding generation diapauses and completes its generation during the following spring), show female-biased sex ratios under direct development and male-biased sex ratios under diapause development²⁴. However, variations in the sex ratios of the butterflies have been attributed to differences in the tendency to diapause between the sexes²⁴.

The first models that related protandry with sexual selection, especially under the condition that females

mate singly^{14,25} fixed the female emergence distribution and estimated optimum protandry by varying the male emergence distribution. The only logic was that selection favoured males to emerge early. The model butterfly, *E. editha*, had sex ratio >1 (refs 14 and 15), which might have worked in favour of the logic. Later models⁹ allowed male and female emergence distributions to vary while optimizing protandry. It was opined that protandry would favour mate maximization in males while minimizing pre-reproductive mortality in females (see 'waiting cost hypothesis'¹); again protandry was prominent when sex ratio was >1 (ref. 9).

Further, we inquired whether the mating system provided sufficient mating opportunities for female *Opisina* moths. The proportion of gravid females (F_g) to the total moths (T) on each night of the flight period (Figure 2) could reveal mating opportunities for females; F_g/T would be inversely related to mating activity. Results indicated that F_g/T was lowest at the beginning and highest at the end (beyond third week) of the activity period (Figure 2), which was partially unexpected (Figure 1). We expected low population densities at the beginning of the flight period to create lower mating opportunity for the early emerging moths, but the results contradicted expectations. Also, F_g/T was expected to be lowest (or mating opportunities to be highest) between the 11th and 19th nights of female activity, which coincided with the peak female, and overall moth activity period. However,

as a large number of females emerged freshly during the peak activity period², it was possible that a considerable number of fresh females might have been sampled, which would give an indication of reduced mating opportunities for females during the peak activity period.

However, importantly, high F_g/T towards the end of the flight period suggested that females active during that period lacked mating opportunities. This was expected because an earlier study² observed that there was no activity of male moths of *Opisina* during the last phase of the flight period. This needed confirmation as it agreed with an important prediction – protandry could lead to loss of mating opportunities especially to the last arriving

females^{9,10,25}. Structure of the population of *Opisina* six nights after the last moth was sampled revealed that females active during the last ~10 nights of the flight period did not contribute to the subsequent generation (Figure 3 shows complete absence of 1st and 2nd larval instars six days after sampling the last moth, which, by working backwards, means that females active during the last ~10 nights of the flight period have not contributed to the subsequent generation). This corroborated expectations from mathematical models that the last females in the flight period of a protandrous population might die as virgins^{9,10,25}. Data (Figure 3) also suggested that females of *Opisina* active during the peak flight period made maximum contribution to the subsequent generation. The early models^{14,26} not only predict protandry in monandrous mating systems but also suggest that female emergence should continue beyond male emergence, which is the case in *Opisina*². The present study goes further ahead to demonstrate that the last females may remain mateless and do not contribute to the subsequent generation. Here, due to female-biased sex ratios and matelessness among last arriving females, natural selection should have acted on females to coincide their emergence with males, if not, emerge earlier to males (protogyny)¹¹.

It appears that males of *Opisina* emerging throughout the flight period have sufficient mating opportunities, and it is the last females that suffer from dying as virgins. As there appears to be no distinct mating advantage for males through protandry, and, as data suggest, selection should have actually favoured early female emergence, it appears that the ‘mate opportunity hypothesis’ also does not explain early male emergence in *Opisina*. On the whole, as of now, there is perhaps no known explanation for protandry in *Opisina*.

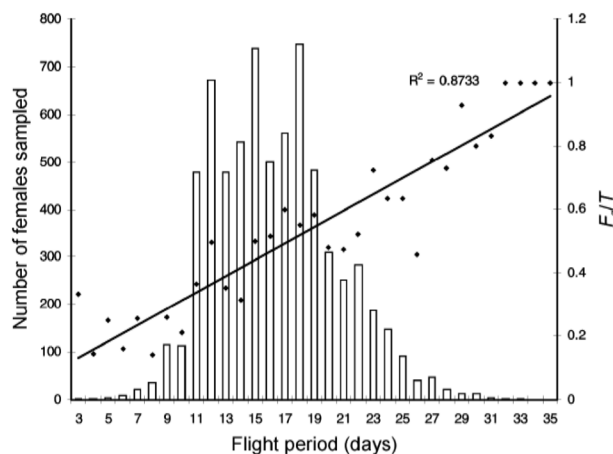


Figure 2. The proportion of gravid females to the total moths sampled (F_g/T ; dots) superimposed on total females sampled (columns) on each night of the flight period (refer Figure 1 for details).

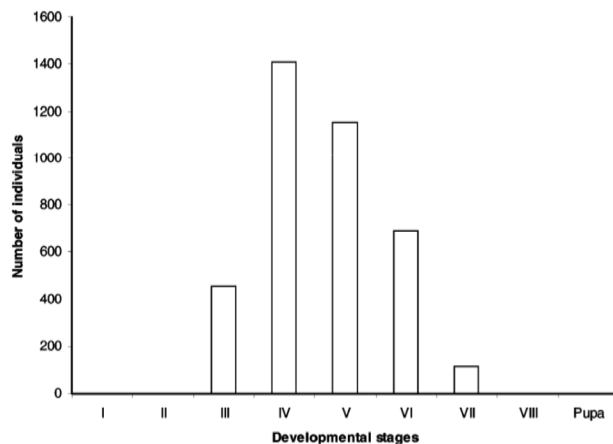


Figure 3. Number of individuals ($n = 3828$) of different developmental stages of *Opisina* present on sixth day after the last female of the previous generation was sampled (larval instars are mentioned in Roman numerals on the X-axis). The last female was sampled on the 35th night of the flight period as in Figure 2. Structure and density of the population was estimated from 15 infested palms; 30 infested leaflets were sampled from each palm. The incubation period for eggs is ~7 days, 1st and 2nd larval instars last ~5 days each^{2,13}.

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