

ing the absence of surface rupture during great and major earthquakes in the Himalaya, we propose that the subduction of sediments play an important role in not allowing the rupture to outcrop near their up-dip termination. Deep drilling in the Andaman and Himalayan regions through the plate boundary interface/detachment and geochemical analyses of the recovered sediment core and modelling of the effects of sediments in controlling the rupture characteristics may possibly provide further evidence in support of this hypothesis.

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Linear sex ratio change in the clutch sequence of *Melopsittacus undulatus*

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Sex ratio, though a significant trait in natural selection, was left open in Darwin's explanations of natural selection. The first explanation for sex ratio being equal was that of Fisher. Since then, several instances of deviation from equal sex ratio have been described both in invertebrates and vertebrates. *Melopsittacus undulatus* is an exotic monogamous pet bird. Male and female on becoming sexually mature form a lifelong pair bond. During the breeding phase of their life (3–4 years) the female lays several egg clutches. Since 2005, 120 pair bonded sets in a sequence of five successive generations were reared. Data on male/female ratio of the 120 pairs showed a definite linear pattern of sex ratio shift among the offsprings across the clutch sequence of the pair bonds. This sex ratio shift is found to be directly correlated to the physiological status and reproductive behavioural courtship display

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of the females. These indicate a causal linkage between the sex ratio shift and female fecundity status.

Keywords: Female courtship displays, linear sex ratio shift, *Melopsittacus undulatus*, physiological status.

SEXUAL reproduction is advantageous as it adds variations to populations for natural selection. Darwin noted that the proportion of males and females in the population is more or less equal, but did not provide any reason for the same. It was Fisher¹ who first explained that sex ratio is approximately equal in the population as a whole, because each future offspring receives genes equally from parents, and the total effort spent on producing the two sexes being equal. Following this, however, several biased sex ratios have been reported with different explanations. Hamilton² observed female biased sex ratio in parasitic wasps that mate in small groups and explained the bias on the basis of local mate competition among males that are genetically related. In higher vertebrates, Trivers and Willard³ found healthy mothers to produce higher proportion of males. In addition to maternal condition, Cockburn *et al.*⁴ attribute the possibility of mothers adaptively manipulating the sex ratio of their offspring based on the assessment of their mate's qualities. Charnov⁵ explains sex ratio as an evolutionarily stable strategy of a population with a bias in production of either sex, where parents investing more in the rarer sex will leave more grandchildren relative to the rest of the population. Meta-analysis of the sex ratio of several ungulate species showed a positive correlation between offspring sex ratio and maternal quality⁶. Incubation temperature, an environmental factor, changes the sex ratio from equality in Australian bush-turkey; at lower temperature the sex ratio is male biased, whereas at higher incubation temperature it is female biased⁷. Among Spanish imperial eagles, there is a deviation of nestling sex ratio that depended on the age of breeding mates⁸ whereas in American kestrels, sex ratio varies with the season. Early in breeding season, the sex ratio of fledgling is male biased, but is increasingly biased towards the female as the season progresses⁹. Pair bond duration of the mates, a behavioural factor, influences the sex ratio in brown thorn bills; females in new pairs produced broods with significantly fewer sons than females in established pairs¹⁰. Male biased broods of blue tits depend on song variables of the male mate¹¹. Thus it is seen that sex ratio is a dynamic inherent trait of animal's sexual reproduction and its deviation from equality is the result of several nonrandom, multidimensionally dependent causal linkages that still remain to be investigated. Hence, the sex ratio of offsprings in the clutches of a large sample of male-female pairs (120 pairs) of the monogamous budgerigar *Melopsittacus undulatus* was evaluated for sex ratio dynamics and possible causal linkages to fecundity status and courtship displays.

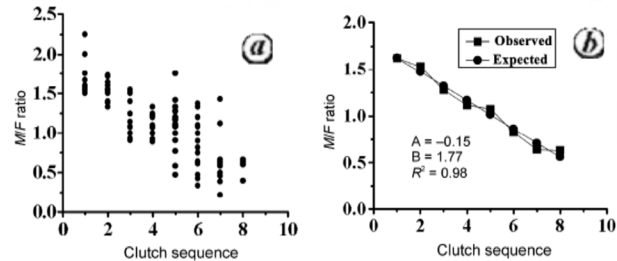


Figure 1. *M/F* ratio of the offspring of successive clutches of five successive generations of the budgerigar, *Melopsittacus undulatus*. *a*, Scatter diagram of the *M/F* ratio of 120 pairs. *b*, Weighted average of the expected and observed *M/F* ratio.

M. undulatus after hatching become sexually mature within 150–180 days. They are not seasonal breeders, but one male and one female after complex behavioural interactions form a pair, remain unseparated as a breeding unit throughout their life. They mate and breed, and the females over a period of four years of her lifetime lays several egg clutches (7–8 clutches). During the courtship and mating for each egg laying bout, they exhibit specific behavioural pattern that comprise autopreening, allopreening, vocalization, beak bite, to and fro shifting, copulation solicitation and beak up. From 2005 onwards, the male/female ratio (*M/F*) of the offspring of 120 pairs of these budgerigars were obtained. The *M/F* ratios of 120 pairs were obtained from six different mating pairs in a sequence of five successive generations (20 sets). Among the total young ones produced by each female of the pair during her lifetime, about 53.7% were found to be males and 46.3% were females. Proportion test of each did not reveal any significant difference in the percentage of males and females ($Z = 0.75$, $P > 0.05$). However, on plotting a scatter diagram of *M/F* ratio of young ones produced by each female in each of their successive 7–8 clutches of the 120 pairs, a linear trend of *M/F* ratio change is noted (Figure 1*a*). This leads to a hypothesis that there is a definite sex ratio shift in the offsprings of *M. undulatus* across their clutch sequence, which can be verified by a suitable theoretical model. As generation of clutch sequence is a function of time, time series model was derived for the prediction of sex ratio of the observed data of the successive clutches of the female budgerigar. The model equation adopted on the basis of least squares theory is

$$Y(T) = AT + B, \quad (1)$$

where $Y(T)$ is the *M/F* ratio of each clutch sequence T . The coefficient A and constant B are estimated values derived from the following two normal equations

$$\sum Y(T) = A\sum T + NB, \quad (2)$$

$$\sum TY(T) = A\sum T^2 + B\sum T, \quad (3)$$

where $\sum T$ is the arithmetic sum of the clutches (1, 2, 3, ..., 8) and $N = 8$.

Solving eqs (2) and (3) gives the estimated values of A and B , for each of the 20 sets. Significance of the A and B were tested by 't' test. Substituting the respective values of A and B in eq. (1) gives the predicted values of M/F ratio of each clutch in 20 sets. The correlation coefficient (R) between the predicted M/F ratio and the observed M/F ratio was calculated. Subsequently, coefficient of determination (R^2) was obtained which suggests the goodness of fit of the constructed model given in eq. (1). In 18 of the 20 sets of pairs (6 each) R^2 was between 0.8 and 0.9, and in the remaining two > 0.6 . Since in all 20 sets of male-female pairs (6 each) R^2 was > 0.6 , the weighted average of M/F ratios of the 20 sets was calculated and fitted with the time series model (1) constructed similarly for the weighted average. R^2 of the M/F ratio of the predicted weighted average and the observed ones are very high (Figure 1 b).

Figure 1 a shows that the M/F ratio shifts from 2.25 to 0.2 in the egg laying clutch sequence in the lifespan of a female. Sex ratio is male biased ($M/F > 1$) in the earlier clutches which means that more males are produced during that phase. In the midphase of the sequence, proportion of males and females is equal. Towards the later phase of her lifespan, more females are produced as evidenced by a female biased sex ratio ($M/F < 1$). Such a linear shift in the sex ratio across the clutch sequence (Figure 1 b) obviously can be a species trait that has some significance.

Several factors such as environmental^{7,9,12,13}, mate phenotype¹⁴⁻¹⁹ and age of the breeding mate⁸ bring about changes in sex ratio. Nutritional factors of the females during the sequence of egg laying led to changes in the sex ratio of gulls²⁰. Sex ratio changes are possible in broods of birds at different time spans of breeding sequence²¹⁻²³. In facultative biparental care system, the sex ratio of the young ones from primary females is male biased; whereas the sex ratio of young ones from secondary females is female biased²⁴. Extra pair mating can also result in either more of males or more of females²⁴⁻²⁶. But the high R^2 , linear M/F ratio shift of the young ones in each of the sequence of 7-8 clutches of *M. undulatus* indicate that it is a phenomenon of the species possibly having some adaptive significance. Frank²⁷ hypothesized behavioural and physiological factors to result in sex ratio changes. This was considered as a hypothesis to search for behavioural and physiological factors that are causally linked with the linear sex ratio shift of these birds.

The female of the pair bond exhibited seven distinct behavioural displays that lead to mating (autopreening, allopreening, vocalizations, beak bite, to and fro shifting, copulation solicitation and beak up). Number of eggs laid in each clutch (clutch size) and percentage of eggs hatched in each clutch (hatchability) were considered as

the measures of physiological factors that are related to fecundity. As in the case of M/F ratio, a time series model was constructed for prediction of the given behavioural and physiological factors for comparison with the observed data. R^2 was found to be high (> 0.6) only for vocalization frequency (VF), beak bite frequency (BF), clutch size (CS) and hatchability (H). The weighted average of VF, BF, CS and H of the 20 groups was arrived at, and compared with the prediction model as in the case of M/F ratio. VF, BF, CS and H showed highly significant linear decrease across the laying sequence (Figure 2). Pearson bivariate correlation (r) of VF ($r = 0.98$), BF ($r = 0.97$), CS ($r = 0.94$) and H ($r = 0.95$) showed high correlation with the sex ratio. This indicates a definitive sex ratio shift in the clutch sequence of the *M. undulatus* that is causally linked with reproductively behavioural and physiological factors of the bird. Considering the physiological factors, it is seen that during the early phase, more males are produced when the reproductive efficiency is high, and more females are produced during the later phase when the female fecundity factors are low. It appears that the offspring sex ratio is influenced by the fecundity status of females. Producing females seem to be less risky during low fecundity, and when it can afford to take chances, it produces males.

The influence of female's fecundity status on its offspring may be of some adaptive value that can contribute to fitness potential. To what extent the sex ratio deviates away from equilibrium at the population level may not be easily ascertained. It may be noted that in the total young ones produced by a female in her lifetime, the percentage of males and females did not differ significantly. In a

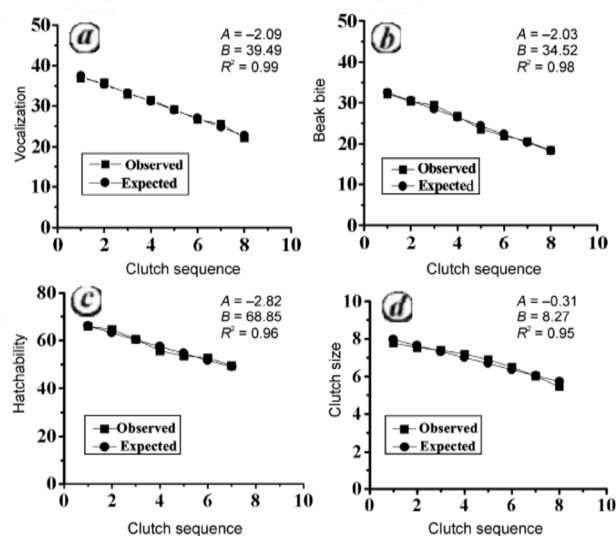


Figure 2. Time series of the expected and observed of the quantitative measures of behavioural and physiological factors across clutch sequence. a, Vocalization frequency. b, Beak bite frequency. c, Hatchability. d, Clutch size.

population of many pair-bonded mating pairs, each would be at its own fecundity status with its consequent fecundity dependent sex ratio in the clutch sequence. But this potential of *M. undulatus* makes it possible for their population sex ratio to regain equal sex ratio, whenever the sex ratio becomes biased, which can happen if the fecundity of majority of the females in that population reduces to a lower status.

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Erratum

Is the biological productivity in the Bay of Bengal light limited?

[S. Prasanna Kumar et al. *Curr. Sci.*, 2010, **98**, 1331–1339]

The caption for Figure 6 should read as follows: ‘Spatial distribution of diffuse attenuation coefficient (m^{-1}) at 490 nm K_d (490) during 10 June to 15 October (top) 2001 and (bottom) 2002. Filled and open circles are CTD and biological station location respectively. See text for details.’

Correction

Cloning of *Sclerotium rolfsii* lection gene and its nematicidal activity

[R. S. Bhat et al., *Curr. Sci.*, 2010, **98**, 1185–1186]

Page 1186, col 1, line 7 should read: ‘from sclerotial bodies¹⁴ (kindly provided by Dr B. M. Swamy, Karnatak University, Dharwad) were also employed for the assay’.