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Changes in the Bird Fauna of Uttara Kannada, India, in Relation to Changes in Land Use over the Past Century

R. J. Ranjit Daniels, N. V. Joshi & Madhav Gadgil*

Centre for Ecological Sciences, Indian Institute of Science,
Bangalore 560012, India

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ABSTRACT

The hilly district of Uttara Kannada (13° 55' N-15° 32' N Latitude and 74° 5' E-75° 5' E Longitude), with an area of 10 200 km², is one of the most forested tracts of south India, although the total area under forest has been reduced from 80% to 70% over the past century. Excellent documentation of the bird fauna exists from the 1890s and 1980s, with a shorter survey conducted in 1938. An analysis of these three surveys suggests that the size of the total bird fauna has remained constant around 465 ± 20 taxa over this period. However, most of the thirty-one resident bird taxa recorded earlier but not sighted in the recent survey, as well as nine taxa observed only recently, are notable habitat specialists. Only a few of these specialists that have probably been lost over this period are forest birds, the majority being characteristic of the drier cultivation and scrub areas. Recent invaders seem to prefer aquatic ecosystems, and it is suggested that this may be a more general pattern. It is therefore vital that more attention be paid to conservation of the biological diversity of the semi-arid tracts of the Indian subcontinent.

INTRODUCTION

While loss of biological diversity, especially in the developing countries of the tropics, has become a matter of worldwide concern, there are relatively

* Author to whom all correspondence should be addressed.

few good field data to support this. Most of the available information is either based on rather incomplete surveys or more complete investigations of relatively restricted areas such as individual islands or forest reserves (Leck, 1979; Brash, 1987; Whitten *et al.*, 1987). The Indian subcontinent is amongst the biologically better known parts of the tropics and its bird fauna has been extensively documented, from Jerdon's (1862-64) pioneering investigations to Ali & Ripley's (1983) authoritative handbook. However, an investigation of the regional changes in India's bird fauna in some depth, against the background of a massive increase in the human population, extensive deforestation and substantial changes in the pattern of land use, has not been possible until now as there have been very few long-term studies of the bird fauna of any region within India, most being based on surveys lasting from a few weeks to a few months and being obviously very incomplete. An important exception to this is Davidson's (1898*a, b*) account of the birds of Uttara Kannada (earlier known as North Kanara/Canara) based on five years' careful observations and collection between 1888 and 1896. The northern part of the same district was resurveyed over a period of three months in 1938 by Koelz (1942). We therefore have an excellent historical record almost precisely from a century and half century ago of the birds of this district. The field studies of R.J.R.D., ranging over a five-year period from 1983 to 1988, provide the most complete regional study of the current bird fauna of India. These three data sets are therefore an excellent basis on which to examine whether there have been significant changes in the bird fauna of this region, and if so what its implications are for a long-term strategy of conserving India's heritage of biological diversity.

THE LOCALITY

The district of Uttara Kannada (13° 55' to 15° 32' N Latitude and 74° 5' to 75° 5' E Longitude), with an area of 10 200 km², lies at the centre of India's west coast where the hill range of Western Ghats, parallel to the coast, is at its lowest and broadest, running all the way to the sea, but hardly ever rising to over 600 m in altitude. The annual rainfall ranges from 350 cm near the coast to 500 cm at some places on the crestline of the hills, but decreases to 120 cm on the eastern edge where the hills merge with the Deccan plateau. Only 1000 km² of the total area are cultivated and 130 km² are orchards. Of the rest, 7000 km² are in different stages of degraded forest and the remainder villages and townships, reservoirs and barren hill tops (Gadgil *et al.*, 1985-86). The forests are well distributed and, except for the heavily settled narrow coastal strip, 80% of the 5 km × 5 km grids into which the district may be divided still retains some forest cover (Pascal, 1984, 1986).

The major transformation undergone by the region over the last century is a reduction in total forest cover from over 8000 km² (Campbell, 1883) to around 7000 km² (Pascal, 1984; Gadgil *et al.*, 1985–86; Kamath, 1985), this land being converted to townships, mines and hydroelectric projects or reservoirs. These changes have largely occurred in the hilly regions away from the coast which were earlier malarial and almost totally under forest cover interspersed with very small enclaves of cultivation and orchards. The first major saw mill was opened in this hilly tract in 1917 followed by a plywood factory in 1944 and a paper mill in 1955. Manganese and iron-ore mining also began in 1955, and by 1983 266 km² of forest land had been cleared. A hydroelectric project along the river Kalinadi in the north of the district has since 1970 destroyed 145 km² of forest. Along the coast more than 25 km² of land was planted with cashew *Anacardium occidentale* and, in the drier eastern parts, at least 70 km² with the Australian blue gum *Eucalyptus* spp. since the 1960s (Kamath, 1985).

Campbell (1883) mentions that there were more than 7000 ponds and tanks in the district, 60% of which were used for irrigation. However, these were all small and shallow and went dry during summer. Furthermore, due to non-availability of cultivators because of the malarial conditions, a 'great deal' of the more than 1000 km² of available cultivable land was lying barren. The development of major irrigation projects since 1956 has brought more than 130 km² of this area from the drier eastern belt under irrigation. The number of wells fitted with electric irrigation pumps has also risen from 39 in 1971 to 5385 at present. As a consequence, what were dry scrub and fallow lands a century ago are now under irrigated cultivation and there are large perennial reservoirs in the driest parts of the district (Kamath, 1985; Gadgil *et al.*, 1985–86; Gadgil & Subash Chandran, 1988).

METHODS

Davidson (1898a), though he spent most of his spare time collecting (by shooting) and identifying birds all over the district, mentions that his list is 'incomplete'. For every bird listed, clear details are provided of geographic distribution, some mention of abundance, commonness and rarity, habitat preference, nesting season and migration. Koelz (1942), on the other hand, collected and identified birds from a small portion (a triangle of c. 25 km on each side) in the north of the district between January and March 1938. Within this short period he listed 232 taxa, most of which are forest-dwellers. For these birds, he recorded some information on geographic distribution, habitat preference, abundance, commonness and rarity, although not as detailed as Davidson's. Koelz did not visit the coastal marshes and

seashores, and thereby almost totally omitted the waders, ducks and other common waterfowl that frequent the district.

The recent survey done by R.J.R.D. was more systematic. Between 1983 and 1988, the entire district was traversed. Birds were sight-recorded during the first two years on 36 1-ha plots distributed over a few localities. The latter part of the survey involved sampling on more than a hundred 600-m long transects laid all over the district, representing most of the major habitat types. In addition, systematic records were kept since 1983 of every bird taxon opportunistically encountered outside the sample limits and while travelling. For each of the 343 taxa encountered during the 5-year period, details of geographic distribution and habitat preference are available. The district was divided into about 500 5 km × 5 km grids and the present patterns of distribution of these birds and the major habitat types were mapped. It seems appropriate in this context to treat a species and subspecies of bird alike. Therefore, the term 'taxon' has been used throughout the text to refer generally to a species or subspecies of bird.

RESULTS

Our basic data set is the sighting of 341 taxa by Davidson (D), 232 by Koelz (K) from a part of the district and 343 by R.J.R.D. (R). These data are analysed, first for all birds, and then for all birds except the saltwater taxa not seen by Koelz (Table 1). There are three possible reasons as to why some taxa were recorded by one of the observers but not by one or more of the others: (1) The taxon was present, but the other observer/s failed to record it; (2) the taxon was not present at the time, but this was a part of the normal turnover of the total bird fauna unrelated to any change in the habitat; or (3) the taxon was not present because its preferred habitat was not available.

TABLE 1
Number of Bird Taxa Recorded by Davidson and/or Koelz^a and/or R.J.R.D. from Uttara
Kannada District

| | Observers | | | | | | Total | |
|-------------------------------------|------------------|------------------|-----|-----|-----|-----|-------|-----|
| | DKR ^b | DKR ^c | DKR | DKR | DKR | DKR | | |
| All taxa | 195 | 9 | 95 | 42 | 17 | 11 | 36 | 405 |
| All taxa except salt-water birds | 195 | 9 | 76 | 35 | 17 | 11 | 18 | 361 |

^a Koelz spent only 3 months on his survey whereas Davidson and R.J.R.D. spent 5 years each.

^b Seen by all three observers.

^c Seen by D & K but not by R and so on.

Preston (1979) suggests a simple model for estimating the number of bird taxa that any particular observer fails to record. He assumes the visibilities of all taxa to be equal and the chances of detecting a given bird by any observer to be the same. If the total number of taxa present in the locality is N , then Np^n would be the number seen by n observers. This model failed to fit ($\chi^2 = 47$) the birds of Uttara Kannada, excluding those of salt water. We then relaxed two of the assumptions of this model: (1) that the three observers were equally efficient in detecting different taxa, since Koelz spent only three months against the five years by the other two observers, and Davidson collected birds, while R.J.R.D only sighted them; and (2) that the chances of all taxa being recorded were equal. We assumed then that the chance of the i th taxon being recorded by j th observer was

$$1 - (1 - V_i)E_j$$

where V_i is the probability of a bird being recorded, and E_j the efficiency of the observer. We further assumed that V was uniformly distributed between 0 and 1, i.e. if the total number of species was N , then the chance of the i th taxon being recorded was i/N . We then have four unknown parameters, E_D , E_K , E_R and N to be estimated from the 7 data points of the second row of Table 1. This model can be fitted to the data ($\chi^2 = 8.3$, $p < 0.05$); as follows: $E_D = 3.27$, $E_R = 2.99$, $E_K = 1.31$, $N = 409$. As expected $E_D > E_R > E_K$. This N excluded salt-water birds. Using the values of E_D , E_R , we can estimate the number of salt-water taxa to be 56. Thus the total avifauna of Uttara Kannada, including those not recorded by any of the three observers, is 465 ± 20 , with a confidence interval at 95% level. This is a plausible estimate. Apart from the 405 taxa recorded by the three observers, there are 14 isolated records in the skin collection of the Bombay Natural History Society or in unpublished checklists of amateur birdwatchers. It is also likely that another 14 taxa recorded from the neighbouring states of Goa, Maharashtra and Kerala, but not yet recorded from Uttara Kannada, may also occur here (Ali, 1969; Grubb & Ali, 1976; Abdulali, 1981). This brings the total number to 433, very close to the lower limit (445) of our estimate.

Therefore, at this level of analysis of the regional bird fauna as a whole, there is no reason to suspect any significant decline in the total number of taxa of birds or change in the composition of the bird fauna. The taxa not recorded in various surveys might have been missed simply because of the necessary incompleteness of the surveys. If this is accepted, however, it follows that those missed are most likely to be those with rather low probabilities of being recorded, namely by being highly cryptic or with small localized populations. In this context it is reasonable to exclude winter visitors from consideration, since many of these visit only occasionally. Thus in 1986, a large flock of about 2000 demoiselle cranes *Anthropoides virgo*

wintered in Uttara Kannada, almost certainly for the first and only time over the century. Similarly a single individual of the greyheaded lapwing *Vanellus cinereus* was recorded in the northeastern part of Uttara Kannada (15° 10' N Lat.) in February 1987, this being its first record south of 25° N Lat. If we therefore omit the wintering species from the analysis of taxa recorded earlier and not recorded by R.J.R.D. and *vice versa*, this leaves us with 31 and 9 taxa respectively (Table 2) of locally resident birds, analysed in Table 3

TABLE 2

List of the 31 Taxa of Birds Not Sighted during the Recent Survey but Recorded Earlier by Davidson and/or Koelz (DUK R) and the 9 taxa Only Recorded Recently by R.J.R.D. (DUK R)

| DUK R | DUK R |
|---|--------------------------------------|
| 1. <i>Gyps indicus</i> | 1. <i>Ardea alba</i> |
| 2. <i>Icthyophaga ichhyaetus</i> ^a | 2. <i>Threskiornis melanocephala</i> |
| 3. <i>Gorsachius melanolophus</i> ^a | 3. <i>Platalea leucorodia</i> |
| 4. <i>Pseudibis papilosa</i> ^a | 4. <i>Glareola lactea</i> |
| 5. <i>Coturnix coromandelicus</i> | 5. <i>Sterna aurantia</i> |
| 6. <i>Perdicula erythrorhynchus</i> | 6. <i>Bubo coromandus</i> |
| 7. <i>Perdicula asiatica</i> | 7. <i>Alauda gulgula</i> |
| 8. <i>Turnix suscitator</i> | 8. <i>Estrilda amandava</i> |
| 9. <i>Turnix sylvatica</i> | 9. <i>Lonchura kelaarti</i> |
| 10. <i>Turnix tanki</i> | |
| 11. <i>Rallus striatus</i> | |
| 12. <i>Rallina eurizonoides</i> | |
| 13. <i>Sypheotides indicus</i> | |
| 14. <i>Rostratula benghalensis</i> | |
| 15. <i>Burhinus oedicephalus</i> | |
| 16. <i>Cursorius coromandelicus</i> | |
| 17. <i>Treron bicinctus</i> | |
| 18. <i>Streptopelia decaocto</i> | |
| 19. <i>Streptopelia orientalis erythrocephala</i> | |
| 20. <i>Psittacula eupatoria</i> | |
| 21. <i>Strix leptogrammica</i> | |
| 22. <i>Taccocua leschenaulti</i> | |
| 23. <i>Centropus toulou</i> | |
| 24. <i>Picus myrmecophoneus</i> | |
| 25. <i>Mirafra javanica</i> | |
| 26. <i>Mirafra assamica</i> | |
| 27. <i>Turdoides striatus somervillei</i> | |
| 28. <i>Turdoides caudatus</i> | |
| 29. <i>Dumetia hyperythra</i> | |
| 30. <i>Zoothera dauma</i> | |
| 31. <i>Aethopyga siparaja</i> | |

^a Recently resighted by amateur birdwatchers.

TABLE 3
Attributes of Birds Recorded in terms of being Habitat Specialists (S), Rare (R) or Cryptic (C)

| Attributes ^a | DUK R ^b | DUK R ^c |
|-------------------------|--------------------|--------------------|
| SRC | 8 | 1 |
| SRC̄ | 9 | 1 |
| S̄RC | 6 | NIL |
| SRC̄ | 1 | 4 |
| S̄RC̄ | 2 | 1 |
| S̄RC | 1 | NIL |
| S̄RC̄ | 4 | 2 |
| S̄RC | NIL | NIL |
| Total | 31 | 9 |

^a SRC, taxon that is a habitat specialist, rare and cryptic; SRC̄, taxon that is a habitat specialist and rare but not cryptic, and so on.

^b Recorded by Davidson and/or Koelz but not by R.J.R.D.

^c Recorded by R.J.R.D. but not by Davidson and Koelz.

according to habitat specialization, cryptic characteristics and rarity. Rarity is defined here as species not seen more than four times, always in very small numbers or in highly localized populations.

Table 3 reinforces the conclusion that being rare or cryptic, and consequently not being recorded, could largely account for the apparent changes in the bird fauna. Nevertheless, it is also apparent that habitat specialization is the single most significant attribute of those birds not recorded at any time. It is thus likely that there have been some actual changes in the composition of the bird fauna of the Uttara Kannada, over and above those that can be attributed to some taxa being missed. Such a change could be due to normal turnover of the taxa, in which case the habitat specialists and generalists utilizing the different habitats would be represented amongst those recorded only earlier or only recently in the same proportion as in the overall bird fauna. Tables 4 and 5 make such an analysis of the resident taxa. It is evident from Table 4 that habitat specialists are represented comparatively more frequently amongst those which have been recorded either only earlier or only recently as compared to the rest. This suggests that transformation of some specific habitat types may be responsible for the observed changes. Table 5 strengthens this conclusion, showing that taxa utilizing dry cultivation and dry rocky hillocks with scrub are represented in a higher proportion amongst the birds recorded only earlier, and those utilizing aquatic ecosystems are represented much more

TABLE 4
Number of Habitats Utilized by Those Resident Birds which have either been Recorded Only Earlier (DUK \bar{R}) or Only Recently (DUK \bar{R}) as Compared to the Remaining 376

| Number of habitats utilised | All birds except DUK \bar{R} & DUK \bar{R} | DUK \bar{R} | DUK \bar{R} |
|-----------------------------|--|-----------------|---------------|
| 1 | 49 (13) | 8 (26.7) | 0 |
| 2 | 118 (31.5) | 12 (40.0) | 1 (11.1) |
| 3 | 74 (19.7) | 4 (13.3) | 5 (55.5) |
| 4 | 61 (16.3) | 4 (13.3) | 2 (22.2) |
| 5 | 36 (9.6) | 1 (3.3) | 1 (11.1) |
| 6 | 12 (3.2) | 0 | 0 |
| 7 | 9 (2.4) | 1 (3.3) | 0 |
| 8 | 6 (1.6) | 0 | 0 |
| 9 | 3 (0.8) | 0 | 0 |
| 10 | 3 (0.8) | 0 | 0 |
| 11 | 0 | 0 | 0 |
| 12 | 1 (0.3) | 0 | 0 |
| 13 | 0 | 0 | 0 |
| 14 | 1 (0.3) | 0 | 0 |
| 15 | 0 | 0 | 0 |
| 16 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 |
| 18 | 1 (0.3) | 0 | 0 |
| 19 | 0 | 0 | 0 |
| 20 | 1 (0.3) | 0 | 0 |
| 21 | 0 | 0 | 0 |
| Total | 375 ^a | 30 ^a | 9 |

Percentages are given in parentheses.

^a For two of the 416 taxa of Uttara Kannada birds no specific habitat description has been given in Ali & Ripley (1983), the basis on which this analysis and that given in Table 5 have been made.

amongst the birds recorded only in the recent survey. As mentioned above, dry scrub/secondary thickets and grasslands were amongst the habitats relatively common in the cultivated tracts of the low-rainfall eastern areas as a result of poor irrigation facilities and cultivation practices at the times of the Davidson and Koelz surveys (Campbell, 1883; Davidson, 1898a; Koelz, 1942). These have subsequently been transformed through extensive irrigation of cultivated lands and planting of other areas by exotic xerophytic species such as *Eucalyptus* and, recently, *Acacia auriculiformis*. At the same time, the district now has a series of reservoirs developed either for irrigation or power generation, greatly increasing the habitat available for birds dependent on larger water bodies. It is therefore likely that the disappearance of species such as the ring dove *Streptopelia decaocto* and

TABLE 5
Utilization of the Different Habitats by those Resident Birds which have been Recorded either Only Earlier ($\overline{DUK R}$) or Only Recently ($\overline{DUK R}$) as Compared to the Remaining 376

| Habitat | All birds except $\overline{DUK R}$ & $\overline{DUK R}$ | $\overline{DUK R}$ | $\overline{DUK R}$ |
|---|---|--------------------|--------------------|
| 1. Humid/wet rocky cliffs/hilltops | 14 (3.7) | — | 1 (11.1) |
| 2. Humid/wet/mixed/semi-evergreen/ secondary evergreen forests | 133 (35.4) | 9 (30.0) | — |
| 3. Humid grasslands | 42 (11.2) | 8 (26.6) | 2 (22.2) |
| 4. Humid/moist degraded/open forests-thickets | 150 (40.0) | 8 (26.6) | 2 (22.2) |
| 5. Humid betelnut/coconut/cocoa/ banana/mixed plantations | 20 (5.3) | — | — |
| 6. Humid/moist exotic tree plantations (<i>Casuarina</i> / <i>Anacardium occidentale</i> / <i>Acacia</i>) | 15 (4.0) | — | — |
| 7. Freshwater marshes/tanks/ reservoirs/paddy fields | 121 (32.2) | 3 (10.0) | 7 (77.8) |
| 8. Freshwater hill streams | 28 (7.5) | 1 (3.3) | — |
| 9. Freshwater rivers | 36 (9.6) | 1 (3.3) | 6 (66.7) |
| 10. Beaches | 53 (14.1) | — | 3 (33.3) |
| 11. Offshore (pelagic) | 14 (3.7) | — | — |
| 12. Estuaries/mangrove/salt pans, etc. | 74 (19.7) | 1 (3.3) | 5 (55.6) |
| 13. Coastal coconut | 7 (1.9) | 1 (3.3) | — |
| 14. Moist/dry teak plantation | 37 (9.9) | 1 (3.3) | — |
| 15. Moist teak-type deciduous forest | 49 (13.1) | — | — |
| 16. Moist/dry <i>Eucalyptus</i> plantations | 18 (4.8) | 1 (3.3) | — |
| 17. Dry deciduous forest | 46 (12.3) | 3 (10.0) | — |
| 18. Dry rocky hillocks with scrub | 92 (24.5) | 14 (46.7) | — |
| 19. Dry cultivation | 121 (32.3) | 15 (50.0) | 2 (22.2) |
| 20. Moist/dry bamboo facies | 29 (7.7) | 3 (10.0) | — |
| 21. Human settlements/habitation | 136 (36.3) | 3 (10.0) | 2 (22.2) |

Percentages are given in parentheses. Since a single taxon may use more than one kind of habitat the percentages add up to more than 100%.

common babbler *Turdoides caudatus* may be related to the loss of habitat. It is also possible that species such as the white ibis *Threskiornis melanocephala* and skylark *Alauda gulgula* are new additions to the bird fauna of the district due to the creation of extensive areas of suitable habitat.

DISCUSSION

Birds utilizing the forest habitat in the Uttara Kannada district appear to be little affected by the changes that have taken place over the last century,

including a decline in the area under forest cover from about 80% to 70% accompanied by an increase in the size of cultivated enclaves and habitation within the forest. Thus, we resighted the single localized population of about 20 birds of the Wynaad laughing thrush *Garrulax delesserti*, a subspecies endemic to the Western Ghats, in the same locality near Castle Rock as had been noted by Davidson and Koelz. Five forest taxa which have apparently disappeared, i.e. the Nilgiri thrush *Zoothera dauma*, the large Indian parakeet *Psittacula eupatoria*, the little scaly-bellied green woodpecker *Picus myrmecophoneus*, the orange-breasted green pigeon *Treron bicincta* and the yellow-backed sunbird *Aethopyga siparaja*, were all rare. Uttara Kannada represents the northern fringe of distribution of *Z. dauma*, and the southern limit for *A. siparaja* (Ali & Ripley, 1983). It is possible that small populations of these species still exist in Uttara Kannada and have been overlooked. By and large, the forest bird fauna of the district has not fared too badly over the last century. The raptors, often noted as most likely to suffer extinction, have also all persisted during the period, the only resident species not recorded by R.J.R.D.—the fishing eagle *Ichthyophaga ichthyaetus*—having been recently resighted by amateur birdwatchers (Bruno Boedts, pers. comm.). As in Java, the raptors appear able to adapt to living in smaller habitat fragments (Thiollay & Meyburg, 1988).

Birds on the fringes of their geographical distribution, those with special habitat preferences, birds of larger size and birds hunted by man for food have been noted to be particularly susceptible to extinction (Diamond, 1971, Terborgh, 1974). Apart from the thrush *Z. dauma* noted above, the ring dove *S. decaocto*, a very conspicuous bird for which the Uttara Kannada district constitutes the western fringe of its distribution, seems now to be extinct. Of the scrub/dryland birds which have apparently disappeared, the lesser florican *Sypheotides indicus*, the Indian courser *Cursorius coromandelicus* and the sirkeer cuckoo *Taccocua leschenaulti* as well as *S. decaocto* are all amongst the largest of the scrub/dryland specialists. They also all happen to be hunted by man for food.

King (1978) notes that of the birds on decline in the world 67.2% are forest birds, 16.8% scrub and grassland birds and 12.7% frequent wetlands. For Uttara Kannada the second category seems clearly to be the most threatened. This is likely to be true also of the country as a whole for, as Table 6 shows, the natural vegetation of the semi-arid and arid tracts of the country has been subject to the highest level of degradation. Consequently, the list of threatened bird forms of the Indian subcontinent as it appears in the recent compilation by the World Conservation Monitoring Centre (1988) includes six taxa characteristic of scrubland habitat, prominent amongst which are the Great Indian bustard *Choriotis nigriceps*, Bengal florican *Eupodotis bengalensis* and the Jerdon's courser *Cursorius bitorquatus*. While some serious thought has been given to the conservation of the desert

TABLE 6
Extent of Potential Area, Closed Canopy Forest, Forest Including Degradation Stages, and Nature Reserves in Major Zones in India

| Zone | Attributes | Potential | Closed canopy | All forest | Nature reserves |
|----------------------|-------------------------|-----------|---------------|------------|-----------------|
| Arid | Area ^a | 481.3 | 0 | 2.2 | 8.2 |
| | Percentage ^b | 17.2 | 0 | 0.1 | 10.0 |
| | Ratio ^c | — | 0 | 0.006 | 0.6 |
| Semi-arid | Area | 670.0 | 17.6 | 31.4 | 7.8 |
| | Percentage | 23.9 | 5.1 | 6.7 | 9.6 |
| | Ratio | — | 0.21 | 0.28 | 0.4 |
| Peninsular deciduous | Area | 1 291.2 | 195.5 | 283.3 | 50.0 |
| | Percentage | 46.1 | 56.6 | 60.7 | 61.6 |
| | Ratio | — | 1.23 | 1.32 | 1.34 |
| Peninsular evergreen | Area | 62.0 | 14.1 | 16.4 | 3.6 |
| | Percentage | 2.2 | 4.1 | 3.5 | 4.4 |
| | Ratio | — | 1.86 | 1.6 | 2.0 |
| Himalaya | Area | 290.5 | 112.3 | 129.0 | 10.9 |
| | Percentage | 10.4 | 32.6 | 27.7 | 13.4 |
| | Ratio | — | 3.13 | 2.66 | 1.29 |
| Andaman and Nicobar | Area | 6.8 | 5.5 | 5.5 | 0.8 |
| | Percentage | 0.2 | 1.6 | 1.3 | 1.0 |
| | Ratio | — | 8.0 | 6.5 | 5.0 |
| Total | Area | 2 801.8 | 345.0 | 467.8 | 81.2 |
| | Percentage ^d | — | 12.3 | 16.7 | 2.9 |

^a 1000s of km².

^b % of total area in that column.

^c % of actual to potential habitat.

^d % of total area (Gadgil & Meher-Homji, 1986).

biota with the establishment of a Desert Biosphere Reserve, we believe that the semi-arid regions deserve the most urgent attention of those concerned with the conservation of India's biological diversity.

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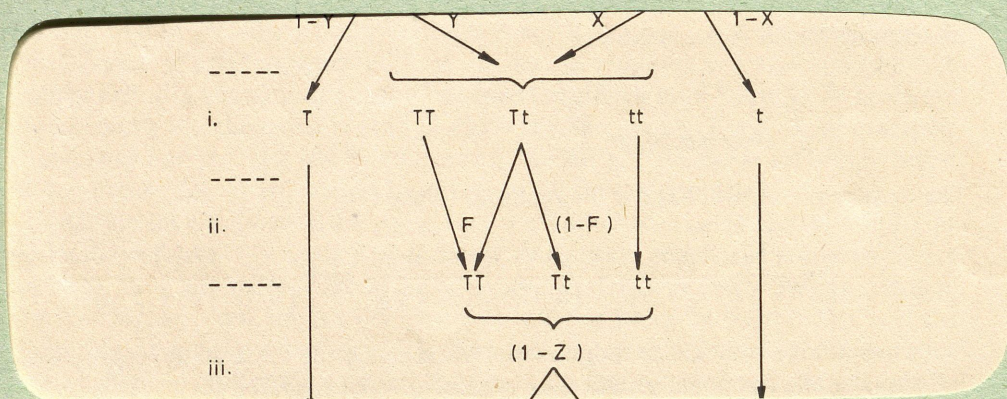
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REFERENCES

- Abdulali, H. (1981). *A Checklist of the Birds of Maharashtra*. Bombay Natural History Society, Bombay.

- Ali, S. (1969). *Birds of Kerala*, 2nd edn. Oxford University Press, Delhi.

- Ali, S. & Ripley, S. D. (1983). *Handbook of the Birds of India and Pakistan*. Compact edition. Oxford University Press, Bombay.
- Brash, A. R. (1987). The history of avian extinction and forest conversion on Puerto Rico. *Biol. Conserv.*, **39**, 97-111.
- Campbell, J. M. (1883). Gazetteer of the Bombay Presidency, **15**(1 & 2). Government Central Press, Bombay.
- Davidson, J. (1898a). Birds of North Kanara, Part I. *J. Bombay Nat. Hist. Soc.*, **11**, 652-79.
- Davidson, J. (1898b). Birds of North Kanara, Part II. *J. Bombay Nat. Hist. Soc.*, **12**, 43-72.
- Diamond, J. M. (1971). Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. *Proc. Natn. Acad. Sci.*, **68**, 2742-5.
- Gadgil, M. & Meher-Homji, V. M. (1986). Role of protected areas in conservation. In *Conservation of Productive Agriculture*, ed. V. L. Chopra & T. N. Khoshoo. Indian Council of Agricultural Research, New Delhi, pp. 143-59.
- Gadgil, M. & Subash Chandran, M. D. (1988). On the history of Uttara Kannada forests. In *Changing Tropical Forests*, ed. J. Dargavel, K. Dixon & N. Semple. Centre for Resource and Environmental Studies, Canberra, pp. 47-58.
- Gadgil, M., Hegde, K. M. & Shetty, K. A. B. (1985-86). Uttara Kannada: A case study in hill area development. In *Karnataka State of Environment Report 1985-86*, ed. C. J. Saldanha. Centre for Taxonomic Studies, Bangalore, pp. 155-72.
- Grubb, R. B. & Ali, S. (1976). The birds of Goa. *J. Bombay Nat. Hist. Soc.*, **73**, 43-72.
- Jerdon, T. C. (1862-64). *Birds of India*, 2 vols (3 parts). Calcutta.
- Kamath, S. U. (1985). *Gazetteer of India: Uttara Kannada*. Government of Karnataka, Bangalore.
- King, W. B. (1978). Endangered birds of the world and current efforts toward managing them. In *Endangered Birds*, ed. Stanley A. Temple. Croom Helm, Wisconsin, pp. 9-17.
- Koelz, W. (1942). Notes on the birds of the Londa neighbourhood, Bombay Presidency. *J. Bombay Nat. Hist. Soc.*, **43**, 11-38.
- Leck, C. F. (1979). Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. *Auk*, **96**, 343-52.
- Pascal, J. P. (1984). *Vegetation map of South India*. Karnataka Forest Department and French Institute, Pondicherry.
- Pascal, J. P. (1986). Explanatory Booklet on the Forest Maps of South India, French Institute, Pondicherry.
- Preston, F. W. (1979). The invisible birds. *Ecology*, **60**, 451-4.
- Terborgh, J. (1974). Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, **24**, 715-22.
- Thiollay, J. M. & Meyburg, B. U. (1988). Forest fragmentation and the conservation of raptors: A survey on the island of Java. *Biol. Conserv.*, **44**, 229-50.
- Whitten, A. J., Bishop, K. D., Nash, S. V. & Clayton, L. (1987). One or more extinctions from Sulawesi, Indonesia? *Conserv. Biol.*, **1**, 42-8.
- World Conservation Monitoring Centre (1988). *India: Conservation of Biological Diversity*. IUCN/WWF/UNEP, Cambridge.



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Transposable element-mediated evolution of sex: A population genetic model

N. V. JOSHI

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

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Abstract. For a population made up of individuals capable of sexual as well as asexual modes of reproduction, conditions for the spread of a transposable element are explored using a one-locus, two-haplotype model. The analysis is then extended to include the possibility that the transposable element can modulate the probability of sexual reproduction, thus casting Hickey's (1982, *Genetics* 101: 519–531) suggestion in a population genetics framework. The model explicitly includes the cost of sexual reproduction, fitness disadvantage to the transposable element, probability of transposition, and the predisposition for sexual reproduction in the presence and absence of the transposable element. The model predicts several kinds of outcome, including initial frequency dependence and stable polymorphism. More importantly, it is seen that for a wide range of parameter values, the transposable element can go to fixation. Therefore it is able to convert the population from a predominantly asexual to a predominantly sexual mode of reproduction. Viewed in conjunction with recent results implicating short stretches of apparently non-coding DNA in sex determination (McCoubrey *et al.* 1988, *Science* 242: 1146–1151), the model hints at the important role this mechanism could have played in the evolution of sexuality.

Keywords. Selfish DNA; transposable elements; evolution of sex.

1. Introduction

The existence of mobile genetic elements in eucaryotic organisms has been known for many years (see Shapiro 1983, Berg and Howe 1989). Many conjectures have been made about their possible biological function. However, it was pointed out by Orgel and Crick (1980) and Doolittle and Sapienza (1980) that the ability of these mobile genetic elements to transpose (replicate themselves within as well as between genomes) was *sufficient* for them to spread under the action of natural selection; no functional role was *necessary* (see Doolittle 1982 for a critical review). Hickey (1982) described an explicit quantitative model for this process and obtained conditions under which transposable elements (TEs) can spread in a population despite having a fitness disadvantage. More sophisticated deterministic and stochastic models describing the equilibrium copy number of TEs have been described (Ohta and Kimura 1981; Ohta 1981, 1983; Charlesworth and Charlesworth 1983; Langley *et al.* 1983) while Nanjundiah (1985), using one-locus, two-haplotype models, demonstrated the possibility of stable polymorphisms with regard to the presence or absence of a TE. The population genetics of TEs continues to be a flourishing area of investigation (see Charlesworth and Langley 1989, for a recent review).

Hickey (1982) perceptively pointed out that sexuality (more precisely, outbreeding) was essential for the spread of TEs and made the intriguing suggestion that the evolution of sexuality itself may have been facilitated by TEs. The evolution of sex has been one of the most fascinating and challenging problems in biology for more than a century and has led to a variety of imaginative hypotheses (Williams 1975; Maynard Smith 1978; Bell 1982; Stearns 1985; Michod and Levin 1988). However, Hickey's suggestion does not seem to have received widespread attention (see e.g., Stearns 1985, 1990; Bremmerrmann 1985; Charlesworth 1987, 1989). Population dynamics models based on this idea (contagion models) have been explored by Rose and coworkers (Rose 1983; Tremblay and Rose 1985; Kriebler and Rose 1986) as well as by Zinder (1985). They have demonstrated that invasion of an asexual population by a sexual one is possible under a wide range of conditions. However, the conditions required for the sexual type to go to fixation were found to be rather restrictive. Hickey and Rose (1988), in addition to the summary of these investigations, describe considerable supportive evidence in favour of the model. Curiously, an explicit population genetic formulation of this phenomenon has not been investigated in detail. Such a model is explored here.

In this paper I examine the dynamics of TEs which are able to affect the mode of sexuality in the host population. In particular, I consider a population in which a fixed proportion of individuals reproduces sexually and the rest asexually. The presence of a TE is assumed to control this proportion. It is seen that under a suitable range of parameter values, the TE can go to fixation and can convert the population to an exclusively sexual mode of reproduction.

2. The model

To keep the inherent features of the model as simple as possible, an infinite, panmictic population of haploid organisms with discrete non-overlapping generations is assumed. A one-locus, two-haplotype model for transposable elements is considered (Nanjundiah 1985) such that T indicates the presence and t , the absence of a transposable element.

The model is schematically illustrated in figure 1, and definitions of the symbols used in the text are given in table 1. The population is assumed to have two modes of reproduction with only a fraction of individuals able to reproduce sexually. The magnitude of this fraction is assumed to be determined by the presence or absence of T . Thus of the individuals with t haplotype, a fraction X reproduces sexually and of those carrying T , a fraction Y reproduces sexually.

The sexually reproducing individuals intermingle and mate randomly to form diploid zygotes. The cost of sexual reproduction is modelled by the parameter Z such that the relative fitness of sexually reproducing individuals is $(1 - Z)$. This fitness handicap is assumed to be made manifest in the (transient) diploid stage formed by the union of two sexually reproducing haplotypes.

In Tt zygotes, transposition is assumed to occur with probability F so as to convert it to TT . It is this property of transposition which justifies the term 'selfish' or 'parasitic' DNA and enables T haplotypes to spread in the population. Though such elements are known to be present in multiple copies in a genome, analysis is restricted in the present model to the presence of a single copy; additional copies are unlikely

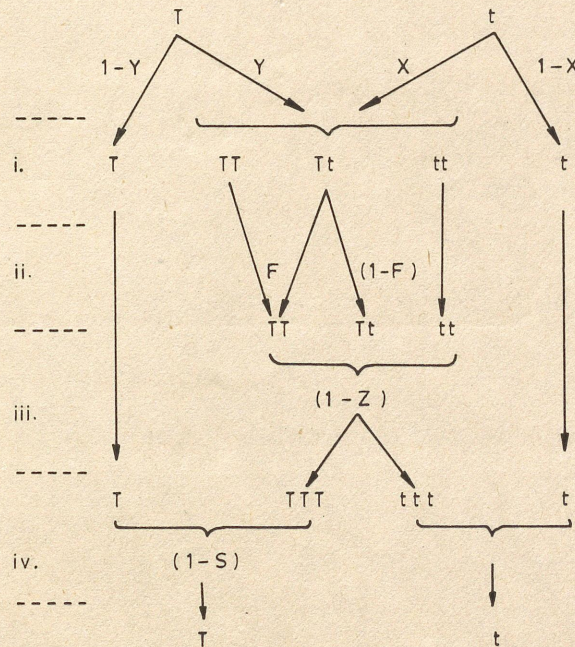


Figure 1. Schematic representation of the model, indicating the different processes responsible for bringing about the change in the frequency of the transposable element T from one generation to the next. The right and left columns depict the asexual pathway for the T and the t haplotypes respectively, while the central column shows the fate of the zygotes. The four stages indicated in the figure are: (i) Zygote formation by random mating in the mating pool formed by the sexually reproducing fractions of T and t ; (ii) transposition in a fraction F of the Tt zygotes, converting them into TT ; (iii) sexual reproduction, with associated cost $(1-Z)$ relative to asexual reproduction; (iv) survival to adulthood, $(1-S)$ for T haplotypes relative to t .

to change the qualitative features of the model. Following Hickey (1982), the T haplotypes are assumed to have a further fitness disadvantage S , such that the relative probability of survival to adulthood is $(1-S)$. Several features of the basic framework of the model are very similar to the model proposed by Hoekstra (1990) for the evolution of male-female dimorphism.

Table 1. Symbols used and their definitions.

| | |
|-------|--|
| T | Haplotype with the transposable element |
| t | Haplotype without the transposable element |
| F | Probability of transposition (conversion of Tt to TT) |
| S | Fitness disadvantage to T haplotype, such that the probability of survival to adulthood is $(1-S)$ |
| X | Fraction of haplotype T which reproduces sexually |
| Y | Fraction of haplotype t which reproduces sexually |
| Z | Cost of sexual reproduction, such that the fitness of sexually reproducing individuals is $(1-Z)$ |
| p | Frequency of haplotype T in the current generation |
| p' | Frequency of haplotype T in the next generation |
| R_T | The rate of growth of the frequency of T haplotypes, i.e. p'/p |
| R_t | The rate of growth of the frequency of t haplotype, i.e. $(1-p')/(1-p)$ |

Let p be the population frequency of T in the n th generation. The frequency p' in the next generation can then be computed as follows. The fraction of the population undergoing sexual reproduction is

$X \cdot (1 - p)$ from genotype t , and

$Y \cdot p$ from genotype T .

The frequencies of tt , Tt and TT zygotes are then

$$\frac{X^2 \cdot (1 - p)^2}{[X \cdot (1 - p) + Y \cdot p]^2}, \quad \frac{2 \cdot X \cdot Y \cdot (1 - p) \cdot p}{[X \cdot (1 - p) + Y \cdot p]^2} \quad \text{and} \quad \frac{Y^2 \cdot p^2}{[X \cdot (1 - p) + Y \cdot p]^2}.$$

With respect to the entire population (of sexually and asexually reproducing individuals), the fractional numbers of zygotes of each kind are, for tt , Tt and TT , respectively

$$\frac{X^2 \cdot (1 - p)^2}{X \cdot (1 - p) + Y \cdot p}, \quad \frac{2 \cdot X \cdot Y \cdot (1 - p) \cdot p}{X \cdot (1 - p) + Y \cdot p} \quad \text{and} \quad \frac{Y^2 \cdot p^2}{X \cdot (1 - p) + Y \cdot p}.$$

Now we can work out the contributions to the next generation from each of the two haplotypes and each mode of reproduction (see figure 1). Denoting the quantity $X \cdot (1 - p) + Y \cdot p$ by C_0 , this goes as follows:

(i) Asexual reproduction of t ,

$$C_1 = (1 - p) \cdot (1 - X).$$

(ii) Sexual reproduction of tt ,

$$C_2 = (1 - p)^2 \cdot X^2 \cdot (1 - Z) / C_0.$$

(iii) Sexual reproduction of untransformed Tt zygotes leading to t ,

$$C_3 = p \cdot (1 - p) \cdot X \cdot Y \cdot (1 - Z) \cdot (1 - F) / C_0.$$

(iv) Asexual reproduction of T ,

$$C_4 = p \cdot (1 - Y) \cdot (1 - S).$$

(v) Sexual reproduction of TT zygotes formed by mating,

$$C_5 = p^2 \cdot Y^2 \cdot (1 - Z) \cdot (1 - S) / C_0.$$

(vi) Sexual reproduction of untransformed Tt leading to T ,

$$C_6 = p \cdot (1 - p) \cdot X \cdot Y \cdot (1 - Z) \cdot (1 - S) \cdot (1 - F) / C_0.$$

(vii) Sexual reproduction from Tt transformed to TT ,

$$C_7 = 2 \cdot p \cdot (1 - p) \cdot X \cdot Y \cdot (1 - Z) \cdot (1 - S) \cdot F / C_0.$$

Finally, p' , the frequency of T in the next generation is given by the equation

$$p' = \frac{C_4 + C_5 + C_6 + C_7}{C_1 + C_2 + C_3 + C_4 + C_5 + C_6 + C_7}. \quad (1)$$

3. Results

The outcome of the competition between T and t can be visualized from figure 2, which depicts p' (the frequency of T in the next generation) as a function of p (the frequency of T in the current generation) based on (1). If, as in figure 2a, p' is always greater than p (i.e. the curve is always above the line $p = p'$), T will always increase in frequency and the TEs will go to fixation. Similarly, if the curve is entirely below the line (figure 2b), T will always be eliminated from the population.

Condition for equilibrium, i.e. $p = p'$ (say $= p^*$) leads to a cubic equation in p^* , as can be derived from (1). Since $p^* = 0$ and $p^* = 1$ always satisfy the condition, there can be at most one more solution with $0 < p^* < 1$; therefore the curve describing p' as a function of p can cut the line $p' = p$ at just one point between 0 and 1. If the equilibrium is a stable one (figure 2c), there will be a stable polymorphism between T and t . If the equilibrium is unstable (figure 2d), the outcome will depend on the initial frequencies of t and T . Since p' is a monotonic function of p [as can be shown from (1)], there can be no cyclic or chaotic behaviour in this system.

Depending on the values of the parameters of the model viz. X , Y , Z , S and F , one of the four outcomes described above is obtained. To arrive at the sets of parameter values which lead to each of these outcomes, the outcome of competition between T and t is explored under two scenarios. In the first, the population is assumed to consist almost entirely of t , and its stability with respect to an invasion by T is investigated. The population can be invaded by T if, as $p \rightarrow 0$, the ratio p'/p is greater than unity.

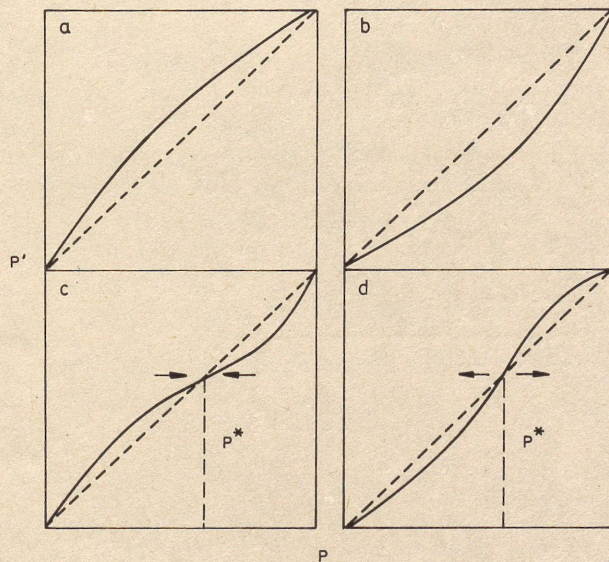


Figure 2. The four theoretically possible outcomes of the competition between T and t as seen from the schematic plots of p' as a function of p (continuous line). (a) T goes to fixation; (b) t goes to fixation; (c) stable polymorphism between t and T ; (d) initial condition dependence such that if initial p is greater than p^* , then T goes to fixation; else t goes to fixation. The broken line corresponds to $p = p'$.

Using $C1 \dots C6$ and (1), this condition can be shown to be

$$R_T = \frac{(1-S) \cdot [1 - Y \cdot Z + F \cdot Y \cdot (1-Z)]}{1 - X \cdot Z} > 1. \quad (2)$$

In the second scenario, the stability of a pure T population is investigated with respect to invasion by t . The invasion by t is successful if the ratio $(1-p')/(1-p)$ is greater than unity as $p \rightarrow 1$ i.e.

$$R_t = \frac{1 - Z \cdot X - X \cdot F \cdot (1-Z)}{(1-S) \cdot (1 - Y \cdot Z)} > 1. \quad (3)$$

The different possible outcomes are

- (i) $R_T > 1$ and $R_t < 1$, T goes to fixation.
- (ii) $R_T < 1$ and $R_t < 1$, initial frequency dependence; both the pure populations stable against invasion.
- (iii) $R_T < 1$ and $R_t > 1$, t goes to fixation, and finally
- (iv) $R_T > 1$ and $R_t > 1$, polymorphism between T and t .

Since the five parameters of the model are restricted to the range $0 - 1$, the entire phase space consists of a five-dimensional hypercube, and the conditions on R_T and R_t divide this hypercube into regions corresponding to the four outcomes.

Any change in the parameter values which increases R_T and decreases R_t can be said to favour the T haplotype (transposable elements). An examination of (2) and (3) reveals that:

- (i) Low values of S (the selective disadvantage of T) favour the spread of T as expected.
- (ii) High values of F (the transposition frequency) favour T .
- (iii) High values of X (the proportion of sexually reproducing t individuals) increase R_T and decrease R_t and thus favour T . This is because higher values of X make more t genomes available for T to take over by transposition in the Tt diploid zygotes.
- (iv) A high value of Y (the proportion of sexually reproducing T) increases R_t and makes a T population more susceptible to invasion by t . This is because a higher proportion of T has to incur the cost of sexual reproduction.
- (v) For both R_T and R_t , the sign of the parameter Z denoting the cost of sexual reproduction is negative both in the numerator and the denominator. The dependence of the outcome on Z is therefore not immediately apparent.

Some special cases, restricting one or more parameters to specific values, are described below.

3.1 Sexual population: $X = Y = 1$

This corresponds to a situation where, regardless of the presence of a TE, the population does not have an asexual mode of reproduction. The expressions (2) and (3), under these conditions, lead to (after some algebra):

$$S < F/(1 + F), \quad \text{for } T \text{ to be able to invade } t \text{ and}$$

$$S > F, \quad \text{for } t \text{ to be able to invade } T.$$

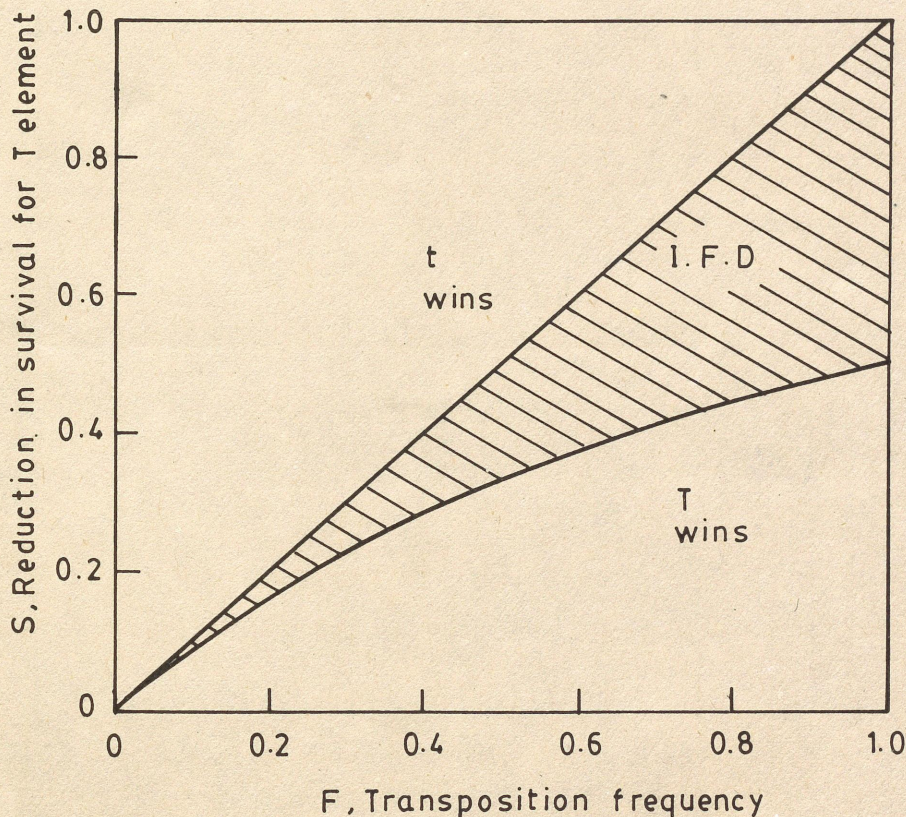


Figure 3. Regions corresponding to different possible outcomes of the competition between T and t in the parameter space of F , the transposition frequency and S , the selective disadvantage to the TEs. The host population is purely sexual ($X = Y = 1$). Hatched regions correspond to initial frequency dependent outcome (IFD) in this and subsequent figures.

Figure 3 illustrates the possible outcomes of the competition in the $S - F$ space. For $F = 1$, the condition for the spread of T is $S < \frac{1}{2}$, as obtained by Hickey (1982). High values of F and low values of S favour T as expected. Interestingly, no combination of S and F can lead to a polymorphism.

Following Nanjundiah (1985), one can explore the effect of the number of copies of T in a diploid zygote on its survival. In particular, S_1 and S_2 can be used to denote the survival of the diploid zygote having respectively one or two copies of the TE. If a single copy is assumed to have no adverse effect on survival, a pure t population becomes more susceptible to invasion by T , and for a suitable combination of values of F and S_2 , a stable polymorphism between t and T is obtained. This result is consistent with that of Nanjundiah (1985).

3.2 No effect on sexuality: $X = Y$

A population with both sexual (fraction X) and asexual ($1 - X$) modes of reproduction is considered, where these proportions are not altered by the presence or absence of TE. Under these conditions, a pure population of t can be invaded by the transposable

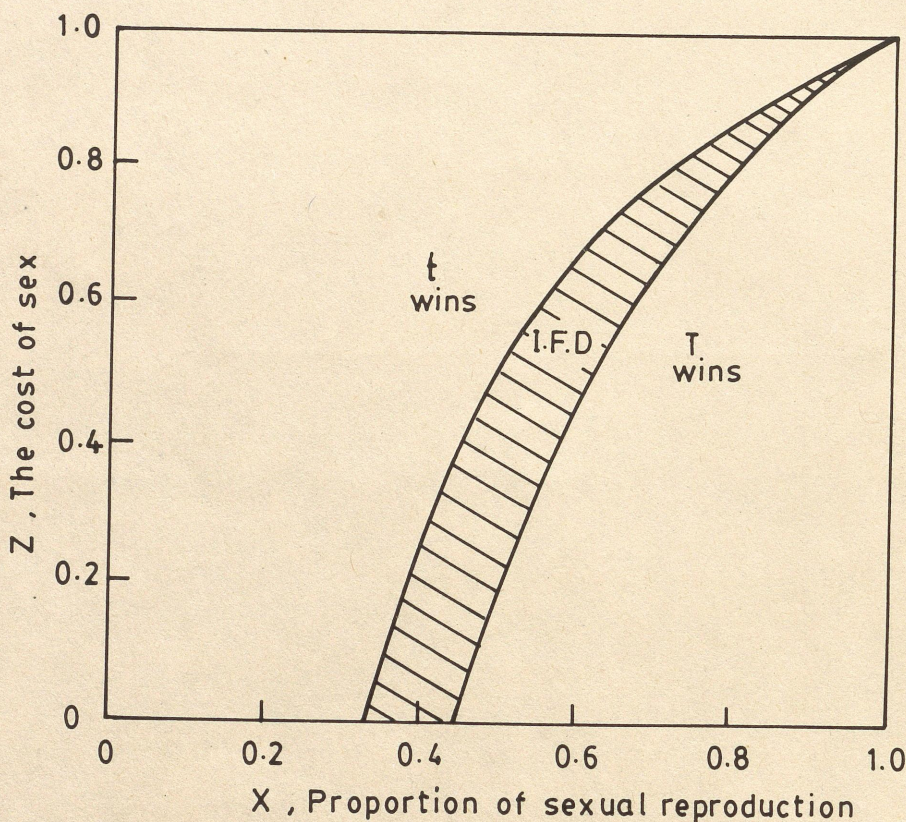


Figure 4. Regions corresponding to different possible outcomes of the competition between T and t in the parameter space of X , the proportion of sexual reproduction and Z , the cost of sexual reproduction relative to asexual reproduction. The proportion of sexual reproduction is independent of the presence of T ($X = Y$). Values of the other parameters are: $F = 0.75$ and $S = 0.25$.

element if

$$Z < \frac{F \cdot (1 - S) - S/X}{F \cdot (1 - S) - S}, \quad \text{for } S < F/(1 + F).$$

However, for $S > F/(1 + F)$, t is stable in the entire ($Z - X$) plane. Similarly, a pure population of T is unstable if

$$Z > \frac{(F - S/X)}{(F - S)}.$$

As shown in figure 4, high Z (cost of sex) promotes t while high X (proportion of reproduction that is sexual) promotes T , as explained earlier. Here, too, a stable polymorphism is not possible.

3.3 Evolution of sexuality: $Y = 1$

This corresponds to a situation where a host population has both the modes of reproduction, whereas the presence of TE makes sexual reproduction obligatory. A

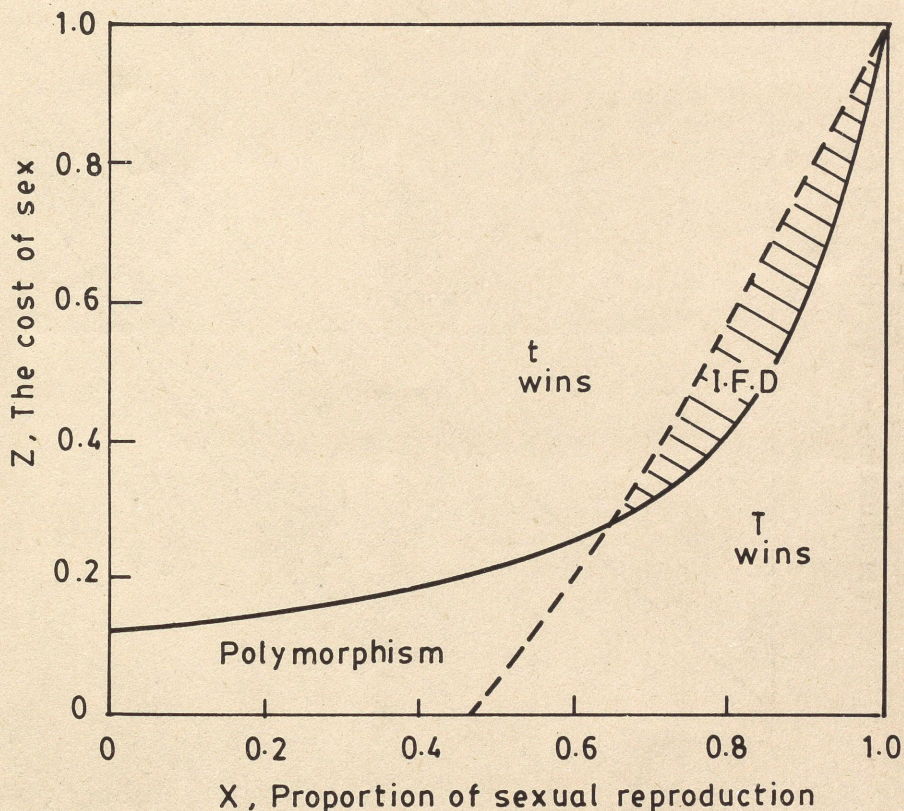


Figure 5. Same as figure 4, except that the presence of transposable elements renders the host purely sexual ($Y=1$). Values of the other parameters are: $F=0.75$ and $S=0.35$.

pure t population is invadable by T if

$$Z < \frac{(1-S) \cdot (1+F) - 1}{(1-S) \cdot (1+F) - X},$$

provided $S < F/(1+F)$; otherwise, t is stable in the entire range of combinations of Z and X . Similarly, T is invadable by t if

$$Z > \frac{F \cdot X - S}{(1-S) - X \cdot (1-F)}.$$

As seen from figure 5, all the four possible outcomes mentioned earlier, i.e. T winning, t winning, initial frequency dependence, and stable polymorphism, can be realized, depending on the values of X and Z . As before, high Z favours t and high X favours T .

To reiterate, in the region corresponding to high X and low Z , a population of t individuals capable of reproducing both sexually and asexually ($0 < X < 1$), has been taken over by T , which reproduces exclusively sexually ($Y=1$). The model thus demonstrates the feasibility of transposable element-mediated evolution of sexuality.

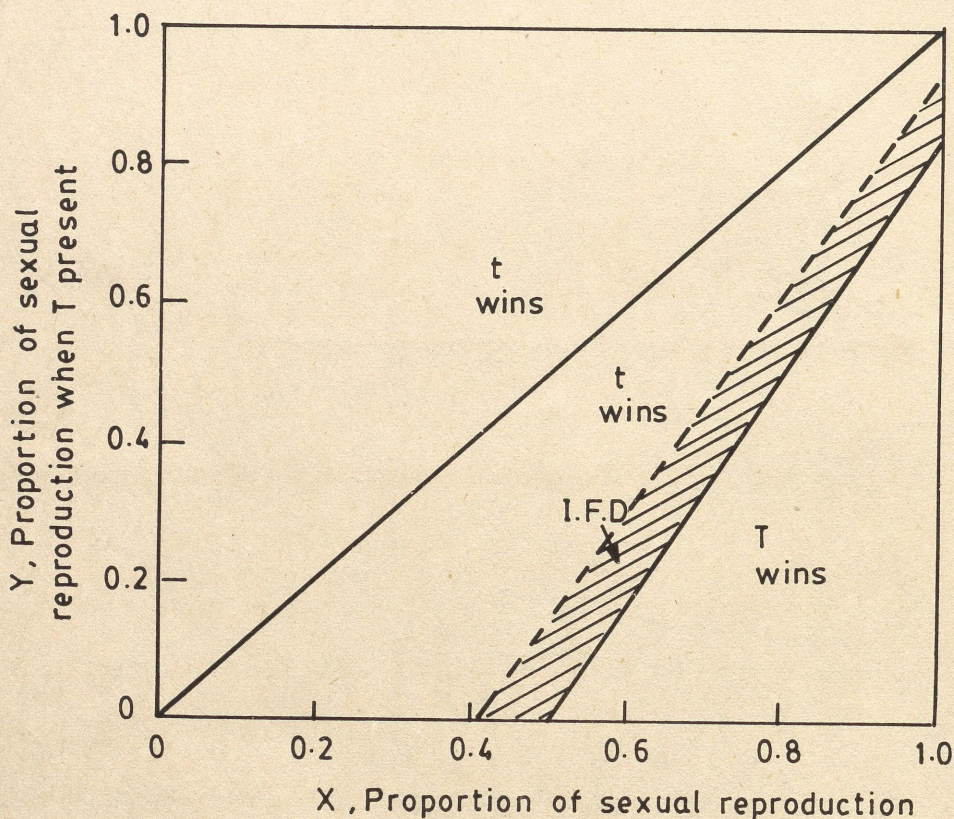


Figure 6. The outcome of competition between T and t in the parameter space of X , the proportion of sexual reproduction in the absence of TEs and Y , that corresponding to the presence of TEs. Values of the other parameters are: $F = 0.20$, $S = 0.25$ and $Z = 0.50$.

3.4 Suppression of sexuality by TEs: $Y < X$

The outcome of competition between t and T is shown in figure 6 in the $(Y - X)$ space, to indicate the effect of different levels of modulation of sexuality by T . The figure shows that for a suitable combination of parameters (corresponding to the bottom right corner of the diagram), T can go to fixation for $Y < X$. If a high cost of sexual reproduction is coupled to a low rate of transposition, then a TE which reduces the proportion of sexual reproduction is selected for. In other words, a suppression of sexuality by transposable elements has also been shown to be possible in this model. These arguments can be quantitatively expressed by the condition for the invasion of t by T

$$Y < \frac{S - X \cdot Z}{(1 - S) \cdot [F \cdot (1 - Z) - Z]}$$

if $Z > F/(1 + F)$, and the condition for invasion of T by t

$$Y > \frac{X \cdot (Z + F - F \cdot Z) - S}{Z \cdot (1 - S)}$$

4. Discussion

The models described here consider a population which has both sexual as well as asexual modes of reproduction, the proportion of individuals adopting one or the other mode being modulated by the presence of TEs. The formulation developed here is also applicable to organisms (such as rotifers) in which several cycles of asexual reproduction are followed by one or more cycles of sexual reproduction. The presence of TEs can then modulate the number of generations of asexual reproduction between two episodes of sexual reproduction.

It may be noted, as pointed out by Hickey (1982) and Nanjundiah (1985), that the model can also be used to describe the evolution of outbreeding. This is due to the formal similarity between inbreeding versus outbreeding on one hand and asexual versus sexual modes of reproduction on the other.

What is the experimental evidence supporting the model? Perhaps the most unambiguous demonstration of transposable elements affecting modes of reproduction is seen in yeast (Klar *et al.* 1981, see Hickey and Rose 1988), where the switch between the mating types *a* and α is mediated by the transposable elements *HML_a* and *HMR_a* (see for example, Zubay 1987). In higher organisms, it is difficult to find such clear-cut examples of TEs influencing sexuality. However, several instances are known of mobile genetic elements producing large phenotypic effects related to sexuality (Green 1980; Werren *et al.* 1988). Thus, the *P* elements in *Drosophila* exhibit hybrid dysgenesis when *P* males mate with *M* females but not vice versa. In the fly *Megaselia scalaris* (Green 1980), the maleness-determining genetic element *M* is known to be mobile, capable of transposing to nonhomologous chromosomes. Transposable elements are also known to be capable of moving adjacent stretches of DNA along with them during the process of transposition, and short stretches of DNA (in the form of mobile elements or otherwise) can profoundly influence the sexual phenotype. Perhaps one of the most interesting examples of the role played by short stretches of DNA in sex determination is seen in *Caenorhabditis elegans* (McCoubrey *et al.* 1988), where an increased copy number of an octanucleotide seems to promote feminization of chromosomal males. Such a regulatory function could be performed by the stretch of DNA by serving as a binding site for a regulatory protein (Chandra 1985). In summary, assuming TEs to be capable of influencing the regulatory switch between sexual and asexual reproductive pathways seems quite plausible. It may be worth mentioning that the recent experiments of Stouthamer *et al.* (1990) have demonstrated that certain microorganisms are capable of converting the parasitic wasp *Trichogramma* from a sexual to an asexual mode of reproduction.

The ability of TEs to transpose endows them with a considerable fitness advantage. This can offset other costs incurred by them indirectly by way of a lowered fitness of the host. For example, as modelled here, the cost of sex may be imposed on the host by the TEs by inducing sexuality in hosts which are otherwise mostly asexual. On the other hand, sexuality itself is essential for the spread of TEs. The two properties (ability to transpose and sexuality) are thus capable of positively reinforcing each other. Estimates of the rates of transposition in *Drosophila* (Charlesworth and Langley 1989) indicate rather low values – of the order of 10^{-4} per generation. These are probably too small for the present model to be effective if the cost of sex is substantial. However, these rates are known to increase by an order of magnitude in a suitable genetic background (Good and Hickey 1986) and still higher values do not seem unlikely (Green 1980).

The maximum rate of spread of TEs is obtained when the transposition frequency is unity, and when the host incurs no cost by harbouring TEs. The fitness advantage in this case is $\frac{1}{2}$, just adequate to counterbalance the two-fold cost of sex. It is therefore unlikely that TEs by themselves would be responsible for the evolution of sexuality. However, the cost of sex may be lowered when one or more of the several processes favouring sexuality (e.g. variable environment, hostile coevolution in host-parasite systems etc.; see Stearns 1990) are operative. Thus, acting in conjunction with these processes, modulation of sexuality by the transposable elements is seen to be a very effective mechanism for the evolution of sex.

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References

- Bell G. 1982 *The masterpiece of nature: The evolution and genetics of sexuality* (Berkeley: University of California Press)
- Berg D. E. and Howe M. M. (eds) 1989 *Mobile DNA* (Washington, DC: Am. Soc. Microbiol.)
- Bremermann H. J. 1985 The adaptive significance of sexuality. *Experientia* 41: 1245-1254
- Chandra H. S. 1985 Sex determination: A hypothesis based on noncoding DNA. *Proc. Natl. Acad. Sci. USA* 82: 1165-1169
- Charlesworth B. 1987 The population biology of transposable elements. *Trends Ecol. Evol.* 2: 21-23
- Charlesworth B. 1989 The evolution of sex and recombination. *Trends Ecol. Evol.* 4: 264-267
- Charlesworth B. and Charlesworth D. 1983 The population dynamics of transposable elements. *Genet. Res.* 42: 1-27
- Charlesworth B. and Langley C. H. 1989 The population genetics of *Drosophila* transposable elements. *Annu. Rev. Genet.* 23: 251-287
- Doolittle W. F. 1982 Selfish DNA after fourteen months. In *Genome evolution* (eds) G. A. Dover and R. B. Flavell (London: Academic Press)
- Doolittle W. F. and Sapienza C. 1980 Selfish genes, the phenotype paradigm and genome evolution. *Nature (London)* 284: 601-603
- Good A. and Hickey D. A. 1986 The spread of transposable P elements in mixed P-M populations of *Drosophila melanogaster*. *Genetics* 113: 72
- Green M. M. 1980 Transposable elements in *Drosophila* and other diptera. *Annu. Rev. Genet.* 14: 109-120
- Hickey D. A. 1982 Selfish DNA: a sexually transmitted nuclear parasite. *Genetics* 101: 519-531
- Hickey D. A. and Rose M. R. 1988 The role of gene transfer in the evolution of eukaryotic sex. In *The evolution of sex* (eds) R. E. Michod and B. R. Levin (Sunderland, Mass: Sinauer Associates)
- Hoekstra R. F. 1990 The evolution of male-female dimorphism: Older than sex? *J. Genet.* 69: 11-15
- Klar A. J. S., Strathern J. N., Broach J. R. and Hicks J. B. 1981 Regulation of transcription in expressed and unexpressed mating type cassettes of yeast. *Nature (London)* 289: 239-244
- Kriebler M. and Rose M. R. 1986 Males, parthenogenesis and the maintenance of anisogamous sex. *J. Theor. Biol.* 122: 421-440
- Langley C. H., Brookfield J. F. Y. and Kaplan N. L. 1983 Transposable elements in Mendelian populations. I. A theory. *Genetics* 104: 457-472

- Maynard Smith J. 1978 *The evolution of sex* (Cambridge: University Press)
- McCoubrey W. K., Nordstrom K. D. and Meneely P. M. 1988 Microinjected DNA from the X chromosome affects sex determination in *Caenorhabditis elegans*. *Science* 242: 1146–1151
- Michod R. and Levin B. R. (eds) 1988 *The evolution of sex* (Sunderland, Mass: Sinauer Associates)
- Nanjundiah V. 1985 Transposable element copy number and stable polymorphism. *J. Genet.* 64: 127–134
- Ohta T. 1981 Population genetics of selfish DNA. *Nature (London)* 292: 648–649
- Ohta T. 1983 Theoretical study on the accumulation of selfish DNA. *Genet. Res.* 41: 1–16
- Ohta T. and Kimura M. 1981 Some calculations on the amount of selfish DNA. *Proc. Natl. Acad. Sci. USA* 78: 1129–1132
- Orgel L. E. and Crick F. H. C. 1980 Selfish DNA: The ultimate parasite. *Nature (London)* 284: 604–607
- Rose M. R. 1983 The contagion mechanism for the origin of sex. *J. Theor. Biol.* 101: 137–146
- Shapiro J. A. (ed.) 1983 *Mobile genetic elements* (New York: Academic Press)
- Stearns S. C. 1985 The evolution of sex and the role of sex in evolution. *Experientia* 41: 1231–1235
- Stearns S. C. 1990 The evolutionary maintenance of sexual reproduction: The solutions proposed for a longstanding problem. *J. Genet.* 69: 1–10
- Stouthamer R., Luck R. F. and Hamilton W. D. 1990 Antibiotics cause parthenogenetic *Trichogramma* (Hymenoptera/Trichogrammatidae) to revert to sex. *Proc. Natl. Acad. Sci. USA* 87: 2424–2427
- Tremblay C. and Rose M. R. 1985 Population dynamics of gene transfer. *Theor. Popul. Biol.* 28: 359–381
- Werren J. H., Nur U. and Wu Chung I. 1988 Selfish genetic elements. *Trends Ecol. Evol.* 3: 297–302
- Williams G. C. 1975 *Sex and evolution: (Monographs in population biology)* (Princeton: University Press)
- Zinder N. 1985 The origin of sex: An argument. In *The origin and evolution of sex* (eds) H. O. Halvorson and A. Monroy (New York: Alan R. Liss)
- Zubay G. 1987 *Genetics* (Menlo Park, CA: Benjamin/Cummings)

