and Aegypiinae (Old World vultures), were studied. Although there is a relatively wide range in diploid numbers, the karyotypes in this group constitute a firm unity. There are always only 8 microchromosomes, which are clearly marked off from the large group of macrochromosomes. The latter are of medium to small size and can all be plainly characterized by their centromeric position. The numbers of acro-, meta- and submetacentric macrochromosomes vary from one species to another. Without exception, the *Z* chromosome is one of the longest submetacentrics; the *W* is smaller and less easily recognizable. The highest diploid number so far found (78) occurs in the northern gosh-hawk (*Accipiter gentilis*), the lowest (60) in the bearded vulture (*Gypaetus barbatus*).

Unfortunately, no information is available on the karyotype of the osprey (*Pandion haliaetus*). This could probably throw more light on its real affinities within the order.

Beyond doubt the Falconiformes display a much wider karyological variety than any other avian order. This is the more striking since in birds often clear karyological similarities exist between even widely separated orders[9,10]. The differences between the above groups are so well marked that it seems unjustified to speculate on possible relationships between them. The only obvious tie of a falconiform group to other avian orders concerns the Cathartidae. Recently chromosome complements nearly identical to those of the cathartids were found in representatives of the Gruiformes and Ciconiiformes by HOFFMANN (*Bugeranus carunculatus*)[7] and myself (*Anthropoides virgo*, Figure 2; *Gallirallus australis* and *Phoeniconaias minor*; unpublished work). In this respect it would be of interest also to obtain data of the Pelecaniformes.

The complements of the Accipitridae are most uncommon among birds, because of the extremely low number of microchromosomes. No karyotypes are known in the class Aves, with which they could be compared, neither within nor outside the Falconiformes. The karyology does not add conclusive information on the possible relation between Falconidae and Strigiformes. A falconid chromosome complement could be derived from an owl karyotype[5,9] with no less difficulty than from any other typical bird karyotype. The complement of the secretary bird might suggest some distant relation to the Falconidae with respect to the rough macro-microchromosome division, to the Accipitridae, however, with respect to the high number of biarmed macrochromosomes. Information on karyotypes of Cariamidae may be conclusive as to their possible affinities to *Sagittarius*.

Although the karyological data available now seem to stress separation of the Cathartidae from the Falconiformes, the absence of common traits between the remaining groups and between any of these and any other avian order, leaves the question as to their mono- or polyphyletic origin as yet unanswered. Their most unusual assemblage of karyotypes, however, strongly encourages further studies.

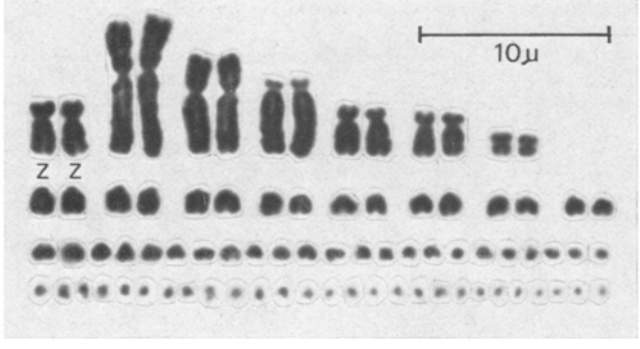

Fig. 2. Karyotype of male *Anthropoides virgo* (Gruiformes).

Summary. Chromosome studies in 4 families of Falconiformes, Cathartidae, Falconidae, Sagittariidae and Accipitridae showed that the karyological variety in this order is much wider than in any other avian order, which underlines the heterogeneous character of the group. Of the 4 families only the Cathartidae show karyological similarities with other avian groups (Gruiformes, Ciconiiformes), while the karyotypes of the Accipitridae are most uncommon among birds, because of the presence of only 8 microchromosomes.

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Male-linked Translocations and the Control of Insect Pest Populations

The simplest of the types of translocation which could be used for insect pest control[1] is one linked to the *Y* chromosome or male-determining gene. Heterozygotes for such male-linked translocations mated to normal females show semi-sterility and produce heterozygous males and normal females, so that the translocation could be automatically perpetuated in a laboratory colony.

A release experiment in a village near Montpellier, with a male-linked translocation in *Culex pipiens*, has been

[1] G. DAVIDSON, *Genetic Control of Insect Pests* (Academic Press, London and New York 1974).

The expected outcome of one generation of breeding in a population containing a male-linked translocation; the translocation is assumed to have no effect on mating competitiveness and to cause 50% sterility

Type of male	Frequency among male parents	Frequency of matings	Fertility of matings	Relative No. of male progeny	Frequency among males in the next generation
Translocation heterozygote	0.8	0.8	0.5	$0.8 \times 0.5 = 0.4$	$0.4/0.6 = 0.67$
Normal	0.2	0.2	1.0	$0.2 \times 1 = 0.2$	$0.2/0.6 = 0.33$
				Total of viable progeny = 0.6	

reported[2–6]. The releases were made in 1970, the translocation frequency in egg rafts was monitored over the following 3 years and it was found to decline steadily (Figure). This was contrary to the expectation of the authors[2,3] who stated that if releases of a 50% sterile translocation produced a translocation frequency among males greater than 67%, its frequency would then increase spontaneously, because more of the male progeny would be translocated than non-translocated. This argument is fallacious, however, and it overlooks the continuing effect of natural selection against the translocation because of its semi-sterility. For example, if releases were terminated with the translocation frequency among males at 80%, the next generation of breeding would be expected to produce the results shown in the Table. The translocation frequency declines to 67% in one generation and further declines would be expected in each subsequent generation of breeding without renewed releases. Assuming a value of 50% for the translocation sterility, one would have expected a faster rate of decline in translocation frequency than was observed (Figure). Thus it is certainly not necessary to invoke immigration from outside the experimental area to explain the decline in translocation frequency[6]. The unexpectedly slow decline observed in translocation frequency may have been due to the evolution of enhanced fertility in the translocation heterozygotes, above their initial value of 50%[7–9]. The Figure also shows a calculation based on an arbitrary assumption about such fertility enhancement, and this calculation fits the observed data.

The aggregate number of genetic deaths as a result of release of a given number of male-linked translocation into an unregulated population would be independent of the level of sterility of the translocation heterozygotes[10] (assuming no differences in mating competitiveness). A relatively fertile translocation would cause low level sterility over many generations, whereas a highly sterile one would cause more sterility initially but would be eliminated quickly. The limit is represented by fully sterile males with which a high degree of sterility is expected initially, without any inheritance.

With both male-linked translocations and sterile males, it is possible, by making sufficiently prolonged releases into a finite population, to reach the point at which all matings are by the genetically altered type of male and this point was reached with a translocation in a caged population[11]. Only if this point is reached, could releases be terminated without the ultimate restoration of a wild type population being inevitable, and a small number of immigrants could always precipitate this process.

Although the eventual total of genetic deaths would be no less with translocations causing low sterility, they are less likely to achieve effective suppression of adult populations than systems causing high sterility, because of compensation by density-dependent larval mortality. Earlier claims[2,4,5] that the 40–45% egg sterility in the experiment near Montpellier led to population suppression, have subsequently been modified[6]. The reduction between 1970 and 1971 in the number of egg rafts collected in ovitraps near the well in which all breeding occurred, can best be explained by a change in the experimental design

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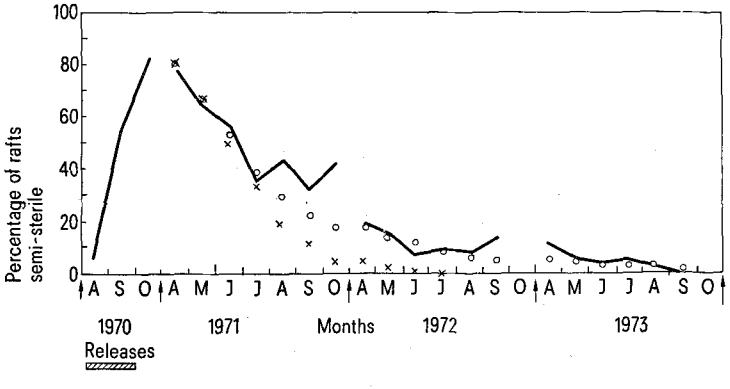

Changes with time in the percentage of egg rafts with semi-sterility: observations[6], solid line; theoretical expectation with 50% fertility in the translocation heterozygote = X; expectation with 50% fertility in the heterozygote rising linearly to 75% over the first five generations = 0. The calculations assume an isolated population, a 1 month generation time in the season April–September/October and an unchanged population composition during hibernation.

between the 2 years[6]. In 1970, females had ready access from the well to the ovitraps via an exit trap in the well lid, from which the mosquitos were liberated outside the well daily. However, in 1971, 1972 and 1973 mosquitos could only leave the well with difficulty because the lid was sealed and the only access was through underground channels[2,6]. The conclusion that the reduced raft collection in 1971, compared with 1970, is not attributable to the effect of the translocation is supported by data[6] showing approximately constant numbers of rafts collected in the ovitraps in 1971, 1972 and 1973, during which period the proportion of translocated rafts declined from 80% to less than 1% (Figure).

The response to natural selection of a male-linked translocation differs from that of an autosomal or *X* chromosome translocation with a viable and fertile homozygote, where the translocation frequency would increase spontaneously if a certain equilibrium is exceeded[12–14]. This property arizes from negative heterosis (i.e. the heterozygote has less fitness than either homozygote) and it does not apply to the male-linked case where the translocation homozygote cannot exist.

Male-linked translocations could persist in populations, or even spontaneously increase, in the following situations: 1. Permanent association of the translocation with greatly enhanced mating competitiveness[10]. Enhanced competitiveness in translocated males was found in a cage experiment[11], but this was apparently due to the conditions under which the translocation material for release was reared and would not therefore be expected to apply in the progeny of released males. 2. Linkage of the translocation to a factor causing segregation distortion in favour males[15–17]. This system could only lead to increase in the translocation frequency if the translocation caused less than 50% sterility; otherwise the output of male progeny from distorter-translocation fathers would be sub-normal and natural selection would favour the normal male-determining chromosome. However, recent field cage tests at this Unit have shown that integration of sex-ratio distortion with translocations improves their ability to suppress a population[18]. 3. Association of the translocation with a 'transport system' based on negative heterosis. Cytoplasmic incompatibility may provide such a system[19], and cage experiments[20] have shown the operation of the principle. However, a polymorphism of cytoplasmic types in Indian *C. fatigans* populations[21] and attenuation of incompatibility with ageing of males[22] can cause recombination of a translocation and the cytoplasmic transport system[20]. Further studies are required to determine whether, by minimizing female releases and ensuring that females have mated before release, the system could achieve effective population control.

Summary. Published data on an experimental release of *Culex pipiens* carrying a male-linked translocation are re-examined and it is shown that the steady decline in translocation frequency after termination of releases agrees with theoretical expectations, because of the selective disadvantage of translocation heterozygote males. Systems based on negative heterosis or meiotic drive are considered whereby it might be possible to prolong the population control which would be achieved by a short term release.

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Karyotype of *Geomys pinetis* (Mammalia: Geomyidae), with a Discussion of the Chromosomal Relationships Within the Genus[1]

Pocket gophers of the genus *Geomys* are fossorial rodents occurring in the central and southeastern United States and northeastern Mexico. Within the genus, RUSSELL[2] recognized two species-groups of recent species. Members of the 2 groups are geographically isolated with the Mississippi River and associated lowlands serving as a barrier between them. All members of the *bursarius* species-group (*bursarius, arenarius, personatus,* and *tropicalis*) have been studied chromosomally. However, none of the members of the *pinetis* species-group (*pinetis, colonus, cumberlandius,* and *fontanelus*) have been karyotyped. Of the species in this group, only *G. pinetis* occupies a large geographic area in the southeastern United States; the other 3 species are known only from highly restricted areas and their systematic relationships to *G. pinetis* are poorly understood.

We have karyotyped 10 individuals of *Geomys pinetis* using techniques described by BAKER[3]. Specimens studied represent 4 currently recognized subspecies – *austrinus, floridanus, mobiliensis,* and *pinetis*. Efforts to obtain the remaining described forms of the *pinetis* species-group were unsuccessful because of scarcity or possible extinction[4]. All individuals that were studied had the same karyotype indicating that there may not be any

[1] Field work was supported by Graduate Dean's Development Fund of Texas Tech University, whereas laboratory phases of the study were supported by the Institute of Museum Research, Texas Tech University. We thank Dr. ROBERT J. BAKER (Texas Tech University) for providing karyological equipment, KATHY WILLIAMS (wife of author) for field assistance, and Mr. RENÉ LAUBACH (Texas Tech University) for translating the summary.
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