

picking up and holding food in one free hand. He also waddles forwards with one or both hands touching overhanging objects but not providing suspensory support for the body. He sometimes moves over short distances with both forelimbs raised and outstretched above his head.

When waddling on a wet floor, he slides his knuckle walking hands in front and without breaking contact with the substrate. As one foot swings forwards, the load is borne almost exclusively on the contralateral foot and haunch.

When moving rapidly on a dry substrate, he raises into a semi-erect quadrupedal position. He places his hands in fist walking postures wherein the fingers are tightly flexed and the skin on the dorsum of proximal phalanges II-V makes contact with the substrate. The hindlimbs are extended and the ischial tuberosities are well above the substrate. The back and head are inclined forwards. The load is borne not only on the lateral aspects of the feet but also on the fists as the subject uses a "diagonal-sequence, diagonal couplets gait"¹.

He moves rapidly on a wet floor with alternate steps of the hindlimbs but without raising his fists from the substrate. Once he briefly slid his right hand forwards in a knuckle walking posture while his left hand remained a fist. The right hand bore only a moderate portion of the load because the forelimbs remained protracted throughout the episode and the body did not pass over the hands.

When leaning forwards to investigate or to pick up orally objects on the floor and when descending head first from low elevations, he consistently places his hands in fist walking postures.

In summary, although Felix often places his hands in knuckle walking postures, he rarely supports a major portion of his body weight on knuckle walking hands. Instead, he places his hands in fist walking postures when support is required for loads that are significantly greater than the weight of the forelimbs themselves. By fist walking he probably avoids stressing metacarpophalangeal joints II-V which, in orangutans, lack special morphological adaptations for knuckle walking of the kind possessed by gorillas and chimpanzees²⁻⁴.

Before 1967, the primatological and anthropological literature was confusing and misleading about the terrestrial hand postures of great apes because some authorities uncritically and sometimes erroneously designated orangutans, as well as chimpanzees and gorillas, "knuckle walkers"⁵.

One of us (R.T.) recently described and classified⁶ the variety of hand postures often used by captive orangutans during terrestrial locomotion, and concluded that only chimpanzees and gorillas should be designated knuckle walkers. He stated that "orangutans do not and, moreover, cannot assume the digitigrade hand posture of the African apes"⁶. This statement should now be qualified and restricted to comparisons between great apes engaged in semi-erect quadrupedal progression with "trot" and "diagonal-sequence, diagonal couplets" gaits¹ on non-lubricated substrates. Although Felix has not been observed to knuckle walk like an African ape or to place his hands in knuckle walking postures during "crutch walking" as do chimpanzees and gorillas, he frequently rests his hands on the middle segments of the fingers and thereby supports on them the weight of his forelimbs and perhaps also a portion of his head and upper torso weight.

Because a highly advanced arboreal climber and arm swinger like an orangutan is able to place his hands in knuckle walking postures suggests that the ancestors of the African apes might have been similarly, or to a greater extent, predisposed to knuckle walking by their own special arboreal heritage.

Man, too, often rests his flexed fingers in facultative knuckle walking postures, as may be witnessed in certain public speakers and football players. Although the thumb is usually used prominently as a supporting strut during human knuckle walking postures, the fact that man has a predisposition for such placement of manual digits II-V may be at least as provocative for evolutionary inferences as the facultative knuckle walking of an orangutan.

It may thus be argued that man passed through a phase of arboreal climbing and suspensory posturing somewhat more advanced than the antibrachiationists and prebrachiationists have admitted into their models^{2,7}. Another optional model would evolve man, orangutans, or both from knuckle walking ancestors. Such a theoretical possibility cannot be ruled out on the basis of available evidence but we do not choose to subscribe to it.

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RUSSELL TUTTLE

Department of Anthropology,
Committee of Evolutionary Biology, and
Biology Collegiate Division,
1126 East 59th Street,
University of Chicago,
Chicago,
Illinois 60637

BENJAMIN B. BECK

Chicago Zoological Park,
Brookfield,
Illinois 60513, and
Biology Collegiate Division,
University of Chicago

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² Tuttle, R. H., *Amer. J. Phys. Anthropol.*, 26, 171 (1967).

³ Tuttle, R. H., *Science*, 166, 953 (1969).

⁴ Tuttle, R. H., in *The Chimpanzee* (edit. by Bourne, G. H.), 2, 167 (Karger, Basle/New York, 1970).

⁵ Straus, W. L., *Amer. J. Phys. Anthropol.*, 27, 199 (1940).

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⁷ Tuttle, R. H., *Sci. J.*, 5A, No. 5, 66 (1969).

Interpretation of Persistence and Effects of Polychlorinated Biphenyls in Birds

Peakall and Lincer¹ suggest that polychlorinated biphenyls (PCBs) found in nature are derived only from highly chlorinated commercial mixtures such as 'Aroclor 1254'. Residues of lower chlorinated mixtures have not been reported in spite of their predominant industrial use. This may be due either to utilization in enclosed systems or to more rapid metabolism or excretion. To demonstrate which residues remain after PCB feeding, pigeons (*Columbia livia*) and Japanese quail (*Coturnix coturnix japonica*) have been fed 'Aroclor' mixtures.

Twenty-four separately caged feral pigeons were fed *ad libitum* for 28 days with wheat dressed with 500 p.p.m. 'Aroclor 1242'. Six control pigeons were fed wheat. At the end of the feeding period six test birds were killed by cervical dislocation and the remainder returned to a diet of mixed grain and pulses before being killed in batches of six at 28, 56 and 168 days. Eighteen 4 week old female Japanese quail were caged in batches of six. One batch was fed *ad libitum* for 20 days with 'Aroclor 1242' dressed food at 250 p.p.m., another with 'Aroclor 1254' dressed food at 250 p.p.m. and the remaining batch left as controls. All birds were killed 24 h after withdrawal of dressed food. This regimen allows comparison with other quail feeding experiments². Immediately after death, breast muscle, liver, brain and omental fat samples were removed from pigeons. Similar samples were removed from quail with the substitution of heart for breast muscle.

Table 1 Mean Total PCB Residues (p.p.m.) found in Quail Tissue after Feeding 'Aroclor 1242' and 'Aroclor 1254' at 250 p.p.m. for 20 Days

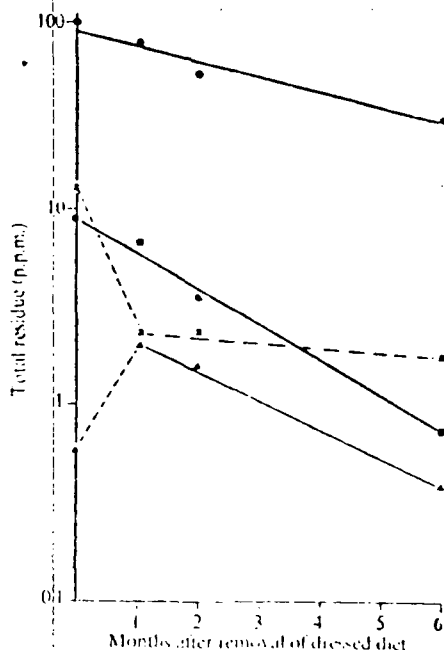
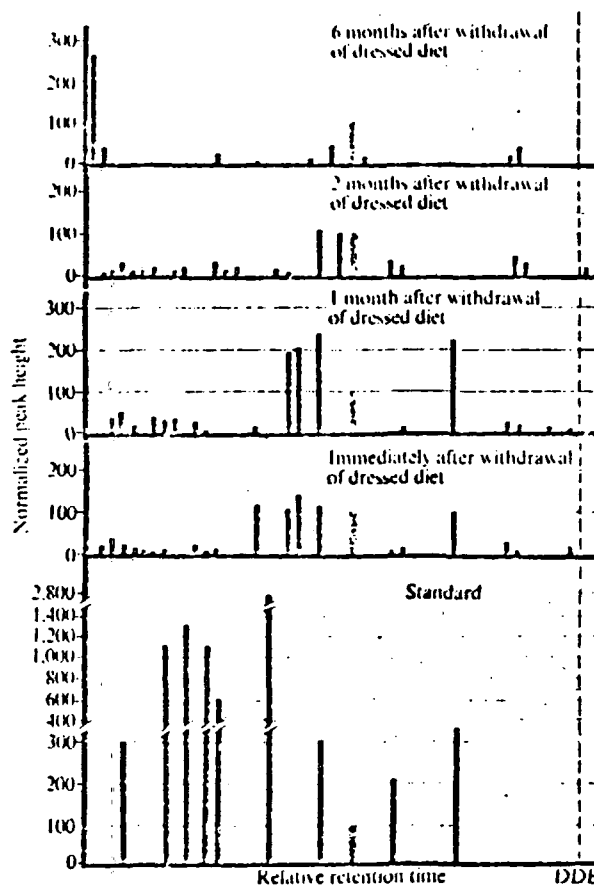
Tissue	'Aroclor 1242'	'Aroclor 1254'
Liver	17.0 ± 2.6*	28.1 ± 7.9
Heart	3.2 ± 0.7	7.0 ± 1.1
Brain	7.8 ± 1.7	7.7 ± 2.3
Omental fat	123 ± 17	304 ± 31

* All figures are mean of six birds ± s.e.

portion of liver was taken for preparation of microsomes² and determination of cytochrome P₄₅₀³ and microsomal protein⁴. The remaining liver and the other tissues were extracted by the method of Taylor *et al.*⁵ before gas-liquid chromatographic analysis using a 3-foot 'Apiezon L' column⁶ at 200° C.

The complex nature of 'Aroclor' mixtures makes the expression of results difficult. Because gross changes have taken place in our experiment we have chosen the method of Risebrough⁷ from those published and compared the sum total of peak heights with a 1,1-di(4-chlorophenyl)-2,2-dichloroethylene (DDE) standard, which in turn was related to a known weight of 'Aroclor 1242'. The mean results obtained from the batches of pigeons are shown in Fig. 1 and from quail in Table 1. Regular checks made on excreta revealed no gross excretion of unchanged material.

The presentation of changes in the gas-liquid chromatographic pattern of PCB isomers is also difficult. Most workers have preferred to suggest that the patterns which they have obtained resemble one of the commercial mixtures, leading to the general conclusion that PCBs remain unaltered in the biosphere. Since we wished to determine whether birds are able to metabolize PCBs we adopted the following method of presentation for gas-liquid chromatographic data. A single peak occurring in all chromatograms from fed birds was selected and represented arbitrarily as 100 units. The mean of peak height for each relative retention time from each batch of birds was normalized to this peak. By this method an average residue "spectrum" can be presented in the form of a

**Fig. 1** Mean total levels of PCB in pigeon tissues following feeding of 'Aroclor 1242' at 500 p.p.m. in diet for 28 days.**Fig. 2** Gas-liquid chromatographic "spectra", normalized to a common peak (stippled column) of 'Aroclor 1242' standard and mean pigeon liver residues following feeding at 500 p.p.m. in diet for 28 days.

line diagram. Fig. 2 shows line diagrams from the livers of pigeons fed 'Aroclor 1242', and Fig. 3 those from quail fed 'Aroclor 1254'. Other tissues gave similar results.

Total PCB residues immediately after withdrawal of treated food show a similar distribution between tissues to those in pigeons fed 1,1-di(4-chlorophenyl)-2,2,2-trichloroethane (DDT)⁸. Allowing for the higher feeding level in the DDT study initial PCB residues are five to ten times higher. In the muscle and fat there is a steady logarithmic decay with half-lives, by inspection, of 50 days and 125 days respectively. After an initial large drop in levels the liver residues also follow a logarithmic decay with a half-life of 140 days. These figures compare with a statistically computed half-life of 28 days for DDT in all pigeon tissues (uncertainty in interpreting PCB analytical results precludes statistical analysis). PCB residues in the brain reach a maximum and then decay logarithmically with a half-life of 50 days. The high liver residue level immediately after withdrawal of food may be attributable to the rate at which liver receives freshly absorbed PCB, and the initial low brain level may reflect the operation of the blood-brain barrier⁹.

Total residues in quail fed 'Aroclor 1242' (Table 1) are higher than those in pigeons in spite of a shorter feeding period at half the level. Food consumption per unit weight of quail, however, is two to three-fold larger than that of pigeons. Residues of 'Aroclor 1254' are generally twice those of 'Aroclor 1242', suggesting that this mixture is more difficult to metabolize or excrete.

The standard 1242 mixture gives a pattern dominated by a few isomers of low retention time on our gas-liquid chromatograph. There is a considerable change in pigeon liver residue patterns (Fig. 2) with peaks of low relative retention times considerably reduced immediately following withdrawal of

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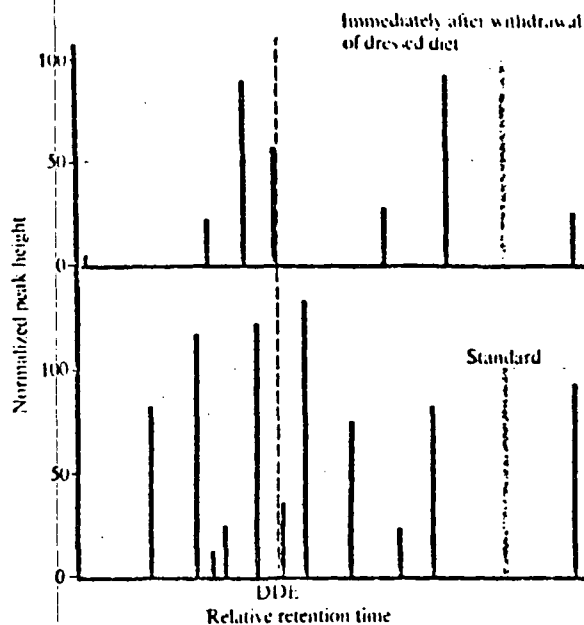


Fig. 3 Gas-liquid chromatographic "spectra", normalized to a common peak (stippled column) of 'Aroclor 1254' standard and mean quail liver residues following feeding at 250 p.p.m. for 20 days.

treated food and virtually absent by the end of the experiment. These peaks seem to be readily removed from the body revealing other minor or less electron capturing constituents with a longer biological half-life. We cannot yet be certain that all these peaks are chlorinated biphenyls present in the original mixture; some may be metabolites. Peaks with a higher retention time are relatively enhanced over the experimental period. The patterns obtained after feeding quail 'Aroclor 1242' have the same general features but 'Aroclor 1254' feeding produces less aberration from the standard.

The conclusion that the less chlorinated isomers are more readily metabolized is also supported by two analyses on a high resolution capillary column. A standard 'Aroclor 1242' exhibited forty-four peaks and a considerable proportion could be assigned structures¹⁰. An extract of fat from a pigeon killed immediately after withdrawal of dressed food exhibited twenty-nine peaks. Most of the fifteen peaks of lowest retention time (mainly dichloro and trichloro isomers) were absent from the extract. Peaks of longer retention time (mainly tetrachloro or higher chlorinated isomers) were present in the pigeon and many were relatively enhanced. These results agree with previous work involving quail¹¹ and rats¹².

The hepatic microsomal systems responsible for metabolizing foreign compounds are sensitive to induction by chlorinated hydrocarbons. The significance of induction is not yet understood but it can be used as an indicator of the biological activity of a compound. Increases in microsomal protein and cytochrome P_{450} are central to microsomal induction and we have measured these to indicate the interference by PCB residues in the normal physiology of the birds (Tables 2 and 3).

Pigeon liver weights remain elevated for at least two months following withdrawal although hepatic microsomal protein returns to normal. In contrast, cytochrome P_{450} levels are still at three times the control level 6 months after returning to normal diet when PCB levels are approximately 2 p.p.m. and composed mainly of higher chlorinated isomers, suggesting that extremely low levels (<1 p.p.m.) of these isomers cause significant elevation of microsomal enzymes. Quail fed either 'Aroclor 1242' or '1254' show similar increases which are far larger than those obtained from similar experiments involving DDT and DDE. 'Aroclor 1254' produces considerably more

Table 2 Mean Liver Weights, Microsomal Protein Levels, Cytochrome P_{450} Levels and Residue Levels for Pigeons fed 'Aroclor 1242' 500 p.p.m. for 28 Days and Killed at 0, 28, 56 and 168 Days after Withdrawal of Dressed Food

Days to death	Mean liver weight (g)	Microsomal protein mg g^{-1} liver	Cytochrome P_{450} nmol g^{-1} liver	Total live residues p.p.m.
Control	$6.97 \pm 0.32^*$	13.70 ± 1.07	2.40 ± 0.28	0
0	10.75 ± 0.98	19.30 ± 1.80	15.47 ± 1.70	15.3 ± 1.8
28	8.78 ± 0.61	17.31 ± 1.51	11.00 ± 1.46	3.6 ± 0.5
56	9.74 ± 0.93	13.47 ± 1.72	7.48 ± 0.83	3.4 ± 0.1
168	6.50 ± 0.45	12.81 ± 1.40	6.73 ± 0.81	1.8 ± 0.2

* All figures are mean of six birds $\pm$ s.e.

Table 3 Mean Liver Weights, Microsomal Protein Levels, Cytochrome P_{450} Levels and Residue Levels for Quail fed 'Aroclor 1242' and 'Aroclor 1254' at 250 p.p.m. for 20 Days before Death

Compound fed	Mean liver weight (g)	Microsomal protein mg g^{-1} liver	Cytochrome P_{450} nmol g^{-1} liver	Total live residues p.p.m.
Control	$3.82 \pm 0.22^*$	25.05 ± 2.27	5.42 ± 0.64	0
'Aroclor 1242'	4.52 ± 0.37	31.62 ± 1.27	22.18 ± 2.83	17.0 ± 2.6
'Aroclor 1254'	5.08 ± 0.22	42.87 ± 1.42	42.21 ± 3.31	28.1 ± 7.9

* All figures are mean of six birds $\pm$ s.e.

induction than '1242', supporting the suggestion above that the more highly chlorinated biphenyls are the most potent inducers.

In spite of analytical and interpretive difficulties we can conclude that pigeons and quail metabolize polychlorinated biphenyls at a rate generally dependent on the amount of chlorine in the molecule. Further work in our laboratory suggests that some lower chlorinated isomers are metabolized extremely rapidly. This could account for the almost universal finding of residues of 'Aroclor 1254' in spite of the major production of '1242'. But biological activity depends on the highly chlorinated isomers, which may need to be taken into account.

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S. BAILEY
P. J. BUNYAN

Pest Infection Control Laboratory,
Ministry of Agriculture,
Fisheries and Food,
Tolworth, Surbiton, Surrey

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