Primatologie, 1998, 1, 179-204

L'automédication chez les singes anthropoïdes : une étude multidisciplinaire sur le comportement, le régime alimentaire et la santé

Michael A. Huffman[1], Riad Elias[2], Guy Balansard[2], Hajime Ohigashi[3] et Peter Nansen[4]

Résumé

L'étude de l'automédication chez les primates non humains éclaire les interactions complexes entre l'animal, les plante et les parasites. Le régime alimentaire des primates comporte parfois un certain nombre de plantes non nutritionnelles contenant des métabolites secondaires et des écorces nutritionnellement pauvres, mais on sait peu de choses sur l'action médicinale possible de ces plantes. Des études récentes sur les grands singes africains suggèrent que l'ingestion d'un certain nombre de plantes non nutritionnelles joue un rôle dans le contrôle des infections parasitaires, soulage et rétablit les désordres gastro-intestinaux en relation avec ces infestations parasitaires. Des études détaillées du comportement, ainsi que des travaux pharmacologiques et phytochimiques, ont été réalisés sur trois populations de chimpanzés africains. Les comportements étudiés consistent en la mastication de la moelle de plantes à goût amer et l'ingurgitation de certaines feuilles entières. Ces deux comportements sont largement répandus chez

1. Department of Social Behavior and Ecology, Primate Research Institute, Kyoto University, Inuyama, Aichi 484 Japan (e-mail: huffman@pri.kyoto-u.ac.jp).
2. Laboratoire de Pharmacognosie, Université de la Méditerranée, Aix-Marseille II, 27 bd Jean Moulin, 13385 Marseille cedex 5, France.
3. Division of Applied Life Sciences, Graduate School of Agriculture, Kyoto University, Oiwke-cho, Kitashirakawa, Sakyo-ku 606-01, Kyoto, Japan.
4. Danish Centre for Experimental Parasitology, The Royal Veterinary and Agriculture University, Bujowsvej 13, 1870 Frederiksberg, Denmark.

toutes les espèces de chimpanzés, y compris le bonobo, ainsi que chez le gorille des plaines. Plusieurs observations montrent que la même plante médicinale est parfois utilisée à la fois par les singes et les humains souffrant de la même maladie. Ces observations nous renseignent sur l'évolution des comportements d'automédication chez l'homme et les premiers hominidés. L'étude de l'automédication chez les anthropoïdes permet de découvrir de nouveaux produits naturels pour traiter d'une manière efficace des maladies parasitaires chez l'homme et les animaux domestiques, ou en captivité.

Mots clés : automédication, anthropoïdes, mastication, ingurgitation, antiparasitaire.
Key words: Self-medication, Great Apes, chewing, swallowing, antiparasite.

INTRODUCTION

Depuis quelques années, un certain nombre d'observations ont relancé l'intérêt des chercheurs pour l'étude de l'automédication chez les animaux (Glander, 1994 ; Huffman et Wrangham, 1994 ; Rodriguez et Wrangham, 1993). L'idée sous-jacente à ce champ de recherche est que les animaux utilisent des plantes contenant des métabolites secondaires ou d'autres substances non nutritionnelles pour se soigner. Les travaux des primatologues sur l'absorbtion de ces plantes visent à déterminer comment et pourquoi les primates sont attirés par ces espèces (Glander, 1975, 1982 ; Hladik, 1977 a et b ; Janzen, 1978 ; McKey, 1978 ; Milton, 1979 ; Oates, Swain et Zantovska, 1977 ; Oates, Waterman et Choo, 1980 ; Wrangham et Waterman, 1981). Une des difficultés de l'interprétation de l'automédication est de faire la distinction entre l'activité des métabolites secondaires présents dans les plantes consommées pour leur valeur nutritionnelle et l'ingestion de produits (plantes ou autres) uniquement pour leurs propriétés médicinales. Même dans les sociétés humaines traditionnelles, la différence entre produit alimentaire et produit médicinal n'est pas toujours très nette, ce qui est clairement exprimé par un proverbe japonais "Isaku dougen", dont la traduction littérale donne "produits médicinaux et nourriture ont une même origine". Un exemple type est celui des épices et des condiments qui sont quotidiennement utilisés dans la cuisine traditionnelle asiatique ; c'est le cas également des algues marines et des rhizomes de gingembre qui sont une source potentielle d'agents antitumoraux (Murakami, Ohigashi et

Koshimizu, 1994, 1996 ; Ohigashi, Sakai, Yamaguchi, Umezaki, Koshimizu, 1992) et d'agents anti-infectieux et antiparasitaires.

Les parasites sont à l'origine de multiples désordres qui affectent le comportement de l'individu et la reproduction (voir par exemple Hart, 1990 ; Holmes et Zohar, 1990), d'où l'importance de remédier à ces affections (cf. Allison, 1982 ; Toft, Aeschlimann et Bolis, 1991). Les effets de la parasitose sur l'hôte et la réponse de l'hôte à l'infection résultent sans doute d'un long processus évolutif (cf. Anderson et May, 1982 ; Ewald, 1994 ; Futuyma et Slatkin, 1983 ; Hamilton, 1964 a et b). Janzen (1978) a été le premier à suggérer que l'ingestion fortuite, par des primates non humains et d'autres animaux, de métabolites secondaires d'origine végétale peut jouer un rôle dans la lutte contre les parasites. Cependant, les grands singes africains nous fournissent des preuves évidentes de l'ingestion volontaire de plantes médicinales, ce qui démontre l'existence de stratégies volontaires d'automédication chez ces primates.

Peut-être en raison de leur proximité phylogénétique, les êtres humains et les chimpanzés utilisent parfois les mêmes plantes pour traiter des symptômes similaires (Huffman, Koshimizu et Ohigashi, 1996). L'étude de l'automédication est donc d'un grand intérêt pour comprendre l'évolution des usages médicinaux depuis les singes anthropoïdes jusqu'à l'homme moderne, en passant par les premiers hominidés. On retrouve également ce comportement chez d'autres espèces de primates et d'autres mammifères.

Cet article vise à la fois à présenter et à analyser un certain nombre d'observations en faveur d'une automédication directe ou indirecte chez les grands singes africains, à proposer des directions pour de futurs axes de recherche, et à prévoir les applications possibles de ces connaissances.

VERS UNE ÉCOLOGIE CHIMIQUE DE L'ALIMENTATION DES ANTHROPOÏDES

Les travaux sur l'automédication des primates ont mis en évidence des comportements d'absorption de plantes à métabolites secondaires, l'ingestion d'écorces et de bois pauvres en nutriments, ainsi que des comportements de géophagie.

Ingestion de fruits et de feuilles à métabolites secondaires

Les chimpanzés, les chimpanzés nains et les gorilles des plaines sont généralement frugivores, mais ils consomment également les feuilles, la

moelle, les graines, les écorces et la sève de plusieurs espèces végétales. Certains métabolites secondaires très intéressants ont été isolés des différentes parties de plantes consommées par ces primates. Ces composés sont généralement considérés comme des moyens de défense du végétal contre les herbivores et les primates (Ehrlich et Raven, 1964 ; Feeny, 1976 ; Howe et Westley, 1988). Ces produits agissent soit directement par leur action toxique sur les animaux, soit indirectement en modifiant la perception des saveurs au niveau du palais, ou en devenant indigestes (Howe et Westley, 1988 ; Wink et al., 1993). Le régime alimentaire des grands singes comprend un certain nombre de plantes appartenant à cette catégorie ; par exemple, les baies de *Phytolacca dodecandra* L. Herit. (Phytolaccaceae) sont des fruits fréquemment consommés par le groupe Kanyawara qui se trouve à Kibale, Ouest de l'Ouganda (voir Wrangham et Isabirye-Basuta, dans Huffman et Wrangham, 1994). Ces baies d'un goût très amer sont riches en saponosides triterpéniques. La dose létale de ces fruits pour la souris et pour le rat est de 2 g. Ces saponines sont actuellement exploitées pour leur activité molluscicide ; l'élimination des mollusques vecteurs de la bilharziose permet une limitation de cette maladie qui sévit en Afrique. Ces saponines ont également une activité antivirale, antibactérienne, antifertilisante, spermicide et embryotoxique (Kloos et McCullough, 1987).

La moelle et le fruit de différentes espèces d'*Aframomum* sont fréquemment consommés par les chimpanzés et les gorilles à travers l'Afrique (cf. Idani et al., 1994 ; Moutsamboté et al., 1994 ; Nishida et Uehara, 1983 ; Sugiyama et Koman, 1992 ; Tutin et al., 1994 ; Wrangham, 1977 ; Wrangham et al., 1993 ; Yumoto et al., 1994). Une étude sur l'alimentation des gorilles de Bwindi (*Gorilla gorilla beringei*, voir Sarmiento, Butynski et Kalina, 1996) est en cours en Ouganda. Cette étude, menée par John Berry (Division of Biological Sciences, Cornell University), consiste à évaluer les activités biologiques des fruits de gingembre sauvage *Aframomum sanguineum* (K. schum.) K. Schum. (Zingiberaceae) ; ces fruits sont également consommés par les gorilles de Kahuzi-Biega, République Démocratique du Congo (ex-Zaïre) (Yumoto et al., 1994). Les essais réalisés sur des homogénéisats de fruits et sur des extraits de graines montrent une activité antimicrobienne significative (Berry, en préparation). Ces fruits sont vendus sur le marché et tout le long des routes de la région de Bwindi. La population locale les utilise comme antifongiques, antibactériens et anthelminthiques (Berry, communication personnelle).

Les jeunes feuilles de *Thomandersia laurifolia* (Y. Anders. Ex Benth.) Baill. (Acanthaceae) sont occasionnellement mastiquées par les gorilles des plaines (*Gorilla gorilla gorilla*) qui vivent dans la forêt de Ndoki du Nord

du Congo (Kuroda, Mokumu et Nishihara, en préparation). Selon Kuroda et ses collègues, les habitants de cette région utilisent les feuilles pour traiter les parasitoses et la fièvre. Les extraits bruts préparés à partir de ces feuilles ont montré une légère activité antischistosomiale (Ohigashi, 1995).

Consommation d'écorces et de bois pauvres en nutriments

Les écorces et le bois sont des parties végétales très fibreuses, hautement lignifiées et parfois toxiques, relativement indigestes et faiblement nutritionnelles (Waterman, 1984). Les chimpanzés et les gorilles consomment rarement certains bois et écorces, et leur rôle dans le régime alimentaire de ces primates reste mal connu (Huffman, 1997). D'après les données ethnopharmacologiques collectées en Afrique, les écorces et le bois de certaines espèces végétales ont une action médicinale intéressante, et leur consommation pourrait faire l'objet d'études comportementales et phytochimiques. Par exemple, les chimpanzés de Mahale mangent les écorces de *Pycnanthus angolensis* (Welw.) Warb. (Myristicaceae), qui sont également utilisées en Afrique de l'Ouest pour ses propriétés purgatives, laxatives, stimulantes digestives, émétiques, et contre les douleurs dentaires (Abbiw, 1990). Des fragments d'écorce de *Grewia platyclada* K. Schum (Tiliaceae) sont mâchés occasionnellement à la fois par les chimpanzés du Mahale et par les habitants de cette région, qui les utilisent contre les douleurs d'estomac (Huffman, 1994). L'écorce d'*Entada abyssinica* Steud. ex A. Rich. (Mimosaceae) est également consommée occasionnellement par les chimpanzés du Gombé et utilisée par les habitants du Ghana comme antidiarrhéique et émétique (Abbiw, 1990) ; celle de *Gongronema latifolium* Benth. (Asclepiadaceae), d'un goût très amer, est parfois mangée par les chimpanzés de Bossou (Guinée). Les tiges de la même plante sont utilisées en Afrique de l'Ouest comme purgatif et pour traiter les douleurs d'estomac et les symptômes liés à des parasitoses intestinales (Burkill, 1985). Enfin, l'écorce d'*Erythrina abyssinica* DC. (Papilionaceae) est occasionnellement consommée par les chimpanzés du Mahale ; les extraits bruts obtenus à partir de cette écorce possèdent une activité antimalarique et antischistosomiale (Huffman et al., sous presse).

En se basant sur des données ethnopharmacologiques (Watt et Breyer-Brandwinjk, 1962 ; Neuwinger, 1996 ; Githens, 1949 ; Kokwaro, 1976), nous avons réalisé une recherche bibliographique sur les plantes alimentaires consommées par les chimpanzés du Mahale (Huffman et al, sous presse), afin de sélectionner les plantes consommées qui pourraient être potentiellement actives dans les parasitoses.

Sur les 192 plantes alimentaires relevées, 172 ont été retenues. Les enquêtes ethnopharmacologiques montrent que, si un certain nombre d'espèces ont de nombreuses utilisations médicinales, 43 d'entre elles (22%) sont utilisées par des populations humaines pour traiter des parasitoses et/ou les désordres gastro-intestinaux qui en découlent. Bien que ces 43 espèces ne soient pas toutes ingérées par les chimpanzés de manière à bénéficier de leurs propriétés médicales, pour 16 d'entre elles les parties végétales consommées par les chimpanzés (feuilles et tiges = 75 %, écorces = 15 %, graines = 5 %, fruits = 5 %) correspondent à celles utilisées par les habitants pour traiter les parasitoses intestinales et les affections gastro-intestinales (Huffman et al., sous presse). La fréquence de consommation de ces 16 espèces est plus importante pendant la saison des pluies (40/56 mois, $z = 22.98$, $p < 0.001$, n = 14 espèces). Il en est de même pour les espèces décrites ci-dessous qui, selon Huffman et al. (1996), sont certainement utilisées contre les vers nodulaires par les chimpanzés du Mahale.

L'automédication n'a pas encore été étudiée chez les orang-outangs du sud est asiatique. Cependant, Galdikas (1988) rapporte que ces animaux consomment l'écorce de 55 espèces végétales différentes. Dans la majorité des cas, c'est la partie interne correspondant à la partie cambiale qui est ingérée. Le plus souvent, l'écorce est mâchée, sucée, et la partie fibreuse rejetée. Il serait prématuré d'attribuer une signification pharmacologique à ce mode d'utilisation chez l'orang-outang, mais cette éventualité ouvre des perspectives pour des recherches futures.

Ainsi, toutes ces descriptions suggèrent que les grands singes consomment certaines parties végétales pour leur action pharmacologique. Il est encore trop tôt pour le confirmer. Cela étant dit, il n'a pas été prouvé clairement que toutes les espèces végétales sont consommées uniquement pour leur valeur nutritionnelle. D'autres études seront nécessaires pour comprendre l'effet préventif de certaines plantes et pour découvrir de nouvelles molécules à visée thérapeutique. Dans le cadre de nos recherches sur les différentes plantes entrant dans le régime alimentaire des singes anthropoïdes, l'étude systématique de l'action antiparasitaire de ces plantes pourrait permettre de découvrir de nouvelles molécules à activité antiparasitaire.

Géophagie

Les comportements de géophagie consistent souvent à consommer de l'argile. L'argile ne contient pas de composants essentiels à la nutrition, tels

que les protéines, les carbohydrates, les lipides et les vitamines. Elle est constituée essentiellement de silicates d'aluminium et de magnésium et/ou de fer. Les principaux types d'argile sont le kaolin, l'illite, la montmorillonite, etc. ; leur principale propriété est de fixer l'eau.

La géophagie est couramment pratiquée par les grands singes, les hommes et de nombreuses autres espèces animales herbivores dans le monde entier (voir par exemple Halstead, 1968 ; Johns, 1990 ; Kreulen et Jager, 1984). D'après les données ethnographiques, l'argile est consommée pour ses propriétés antidiarrhéiques, pour la prévention des douleurs d'estomac ou des vomissements qui sont dus à la consommation, en période de famine, de quantités importantes de plantes riches en métabolites secondaires (Johns, 1990). Chez les primates non humains, la consommation d'argile a pour fonction principale d'absorber les tanins et d'autres métabolites secondaires (Davies et Baillie, 1988 ; Hladik, 1977 a et b ; Müller et al., 1997 ; Oates, 1978). Cependant, la surconsommation d'argile peut donner lieu à une dénutrition et aux perturbations physiologiques qui lui sont liées (voir Halstead, 1968 ; Kreulen, 1985).

Les études d'écologie comportementale et géochimique réalisées chez les gorilles des montagnes, les chimpanzés et les singes rhésus suggèrent que ces primates consomment de la terre pour équilibrer leur régime alimentaire avec les minéraux manquants, et pour soigner les diarrhées dues aux infections parasitaires (Knezevich, 1988 ; Mahaney et al., 1990, 1995 a et b, 1996, 1997). L'analyse chimique des différents sols argileux montre une composition chimique très similaire à celle du Kaopectate, un médicament utilisé dans le traitement des diarrhées et troubles gastro-intestinaux (Mahaney et al., 1990, 1995 a et b, 1996, 1997).

COMPORTEMENTS D'AUTOMÉDICATION CHEZ LES ANTHROPOÏDES

Deux types de comportements liés à l'automédication chez les grands singes africains ont été rapportés : la mastication des moelles végétales à goût amer et l'ingurgitation de feuilles (Huffman, 1997). Dans le cadre de cet article, nous nous intéresserons principalement aux études réalisées sur notre site de recherche dans le parc national de Mahale en Tanzanie (pour plus de détails, voir Huffman, 1997).

La mastication de la moelle végétale amère

A la suite d'observations sur la consommation de *Vernonia amygdalina* Del. (Asteraceae) par des chimpanzés du parc de Mahale manifestement malades, nous avons proposé que la moelle amère mâchée a une fonction curative, ce qui semble confirmé par des tests parasitologiques et phytochimiques (Huffman et Seifu, 1989 ; Huffman et al., 1993).

Vernonia amygdalina est une plante largement répandue en Afrique subsaharienne (Burkill, 1985 ; Dalziel, 1937 ; Watt et Breyer-Brandwinjk, 1962). La mastication de la moelle amère d'autres variétés de vernonia a été également observée à Gombé, Tanzanie (*V. colorata* (Willde.) Drake [Wrangham, 1977] et Kahuri-Biega (*V. hochstetteri* Schi-Bip., *V. kirungae* Rob.E. Fries) [Yumoto et al., 1994 ; Basabose, communication personnelle]).

Dans la forêt de Taï, en Côte d'Ivoire, la moelle amère de *Paliosota hirsuta* (Thunb.) K.Schum. (Commelinaceae) et *Eremospath macrocarpa* (Mann et Wendl.) Wendl. (Palmae) est mâchée occasionnellement par les chimpanzés (Boesch, communication personnelle). Les chimpanzés du parc de Mahale sélectionnent les jeunes pousses de *V. amygdalina*, les débarrassent de leurs écorces et feuilles, pour ne mâcher que la partie interne qui renferme le jus amer. La quantité de moelle consommée à chaque prise est relativement faible ; il s'agit de portions qui varient de 5 à 120 cm de longueur pour 1 cm de diamètre. La durée totale de l'opération est fonction de la quantité de moelle consommée, et se situe généralement entre 1 et 8 minutes (moyenne : 2,9 minutes, $SD = 2.59$, $n = 16$; Huffman, 1997).

Dans le parc national de Mahale, l'usage de *V. amygdalina* a été observé tout au long de l'année, à l'exception des mois de juin et d'octobre, qui correspondent à la fin de la saison sèche (Nishida et Uehara, 1983). Cependant, l'usage de cette plante par les chimpanzés reste un phénomène rare et surtout saisonnier. Il a lieu principalement entre novembre et février, avec un pic maximum en décembre – janvier, c'est-à-dire juste après le début de la saison des pluies.

Une étude menée sur 3 ans a montré que le taux d'infestation parasitaire par *Oesophagostomum stephanostomum* augmente d'une manière significative lors de la saison des pluies, ce qui n'est pas le cas pour les autres espèces de nématodes (Huffman et al., 1996). Les infestations par les vers nodulaires sont plus souvent associées à une augmentation de la fréquence de la consommation de moelle et de l'ingurgitation de feuilles, que les infestations par les autres vers comme *Strongyloides fullebornii*, ou *Trichuris trichiura* (Huffman et al., 1996).

Les observations montrent que les chimpanzés présentent plus de problèmes de santé (diarrhées, malaises, infestations par des nématodes) pendant la période qui correspond à l'utilisation de la plante (Huffman et al., 1996). Dans deux cas où les contrôles étaient rapprochés, on a observé un rétablissement de l'état de santé moins de 20 à 24 heures après la mastication de la moelle (Huffman et Seifu, 1989 ; Huffman et al., 1993). Dans un des cas, où il y avait infestation avec un ver nodulaire, le nombre d'œufs par gramme de fécès (eggs/gr = EPG) a diminué de 130 à 15 en moins de 20 heures. Aucun changement de ce type n'a été observé quand l'infection est due à *Strongyloides fullebornii* (Huffman et al., 1993). Chez la plupart des individus observés pendant la même période, le niveau d'EPG du ver nodulaire a augmenté avec le temps. Ces augmentations observées du taux d'EPG montrent une tendance générale à une réinfection par les vers nodulaires au début de la saison des pluies (Huffman et al., 1997).

L'ingurgitation des feuilles

L'ingurgitation des feuilles est couramment pratiquée dans les cas d'infection à Strongyloides (nématode) pour apaiser les douleurs lors de l'expulsion du ver solitaire. Deux types de mécanismes ont été proposés dans l'élimination des parasites : une action chimique due aux produits naturels contenus dans la plante, et une action mécanique due à la nature de la feuille qui est avalée sans être mâchée (Huffman et al., 1996 ; Wrangham, 1995).

Le comportement d'ingurgitation des feuilles par les chimpanzés a été observé en premier dans les parcs de Gombé et de Mahale (Wrangham et Nishida, 1983) (Figure 1a). Dans ces deux sites, des feuilles entières pliées, non digérées, ont été trouvées dans les fécès des chimpanzés. Il s'agissait de feuilles d'*Aspilia* (syn. *Wedilia*) *mossambicensis* (Oliv.) (Compositae – Asteraceae), *A. pluriseta* (O. Hoffm.) Wild., and *A. rudis* Oliv. et Hiern. Ces observations suggèrent une utilisation non nutritionnelle de ces feuilles. La manière curieuse suivant laquelle les feuilles sont avalées, sans être mâchées, nous laisse penser que les chimpanzés possèdent une pharmacopée sophistiquée (Rodriguez et al., 1985) et attira l'attention des chercheurs de terrain afin de confirmer si des comportements alimentaires anormaux de ce type se retrouvent ailleurs. L'hypothèse de l'action nematocide d'*Aspilia-thiarubrine A* (Rodriguez et Wrangham, 1993) a été écartée depuis cette première observation (Huffman et al., 1996 ; Page et al., 1997).

Figure 1. (a) Un jeune mâle adulte avalant une feuille d'Aspilia mossambicensis. (b) Feuille de Lippia plicata vue au microscope électronique (échelle de la barre = 500 microgrammes).

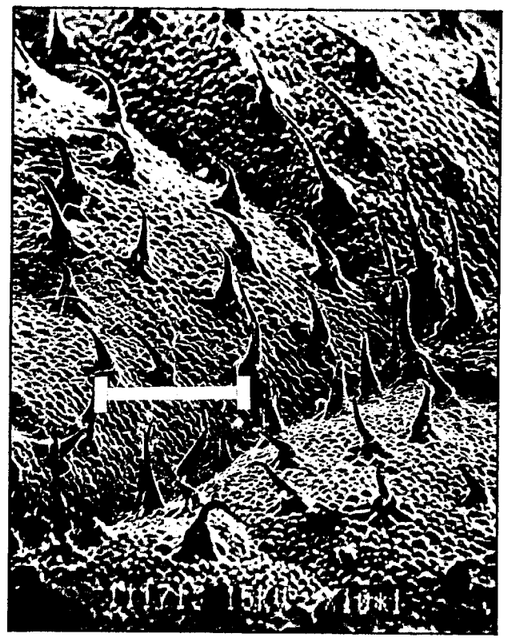

Figure 1. (a) Young-adult male engaged in leaf swallowing of Aspilia mossambicensis. (b) Electron micrograph of Lippia plicata (scale bar = 500 micrograms).

En janvier 1997, on dénombrait jusqu'à 30 espèces végétales dont les feuilles sont avalées par 10 populations de chimpanzés, et une population de gorilles des plaines, dans 10 sites différents à travers l'Afrique (Huffman, 1997). Le type de plantes utilisées est variable ; on trouve des herbacées, des plantes grimpantes, des arbrisseaux, des arbres. Cependant, elles ont toutes un caractère commun au niveau de leurs feuilles, à savoir qu'elles sont velues, avec des surfaces rugueuses (Figure 1b). Les poils sont d'aspect variable, longs, fusiformes, épineux, recourbés en crochets ou regroupés en épis (Huffman et al., 1996).

La moitié distale de chaque feuille est sélectionnée dans un premier temps, pliée avec la langue, lentement tirée avec les lèvres et le palais dans la bouche et avalée entière par le chimpanzé. Chaque animal peut avaler entre 1 à 100 feuilles à la suite. Comme la mastication des feuilles, l'ingurgitation des feuilles est un comportement extrêmement rare.

Les feuilles d'*Aspilia* sont disponibles tout au long de l'année dans les parcs de Gombé et de Mahale, cependant leur usage est plus fréquent au début de la saison des pluies (novembre à mai), avec un maximum d'utilisation (10 à 12 fois plus) en janvier et février (Wrangham et Nishida, 1983). Le comportement de consommation de feuilles est sous certains aspects similaire à celui de la mastication de la moelle amère observé à Mahale. Ainsi, dans le groupe K du parc de Mahale, l'ingurgitation des feuilles est plus fréquente pendant la saison des pluies que pendant la saison sèche (test binomial, $z = 67.41$, $p < 0.0003$; Huffman, 1997), ce qui est également vrai pour les 9 autres espèces du parc dont les feuilles sont avalées de cette manière (Huffman et al., 1997).

Lors d'une observation qui a duré quatre mois (de décembre 1993 à février 1994), nous avons étudié le comportement et l'état de santé des singes, en même temps que l'acte d'ingurgitation des feuilles. Sur les 8 chimpanzés que nous avons observés, 7 ont montré des signes de diarrhée et de malaise pendant la période où les feuilles étaient ingurgitées (Huffman et al., 1996). Quatre-vingt trois pour cent des chimpanzés qui avalaient les feuilles étaient infestés avec un nématode confirmé par le contrôle des fécès (Huffman et al., 1996, 1997). Les vers retrouvés ont été identifiés comme étant des vers nodulaires. Une relation étroite a été établie entre l'ingurgitation des feuilles et l'expulsion des vers nodulaires.

Entre 1993 et 1994, nous avons étudié 254 fécès, dont 9 contenaient des vers. Six d'entre elles contenaient à la fois des vers et des feuilles entières non digérées de *A. mossambicensis, Trema orientalis* (L) Blume syn. *T. guineensis* ou *Aneilema aequinoctiale* (P. Beauv.) Loudon. Le rapport entre la présence des vers nodulaires et des feuilles était hautement significatif

(test exact de Fischer, $p = 0.0001$, Huffman et al., 1996). Dans une fécès, deux vers étaient solidement fixés par les poils à la surface d'une feuille d'*A. aequinoctiale*. La majorité des autres vers étaient piégés à l'intérieur des feuilles pliées. Tous les vers étaient vivants et mobiles, ce qui écarte la possibilité d'une action chimique par les composants des feuilles. Ainsi, l'élimination des vers par une action mécanique des feuilles semble être l'hypothèse principale expliquant l'ingurgitation des feuilles (Huffman et al., 1996).

ETHNOPHARMACOLOGIE ET PHARMACOGNOSIE DE L'AUTOMÉDICATION DU SINGE

La mastication des moelles amères

Plusieurs groupes ethniques africains confectionnent une préparation à base de *V. amygdalina* pour traiter les fièvres paludiques, schistosomiases, la dysenterie amibienne et plusieurs autres parasitoses intestinales et les douleurs d'estomac (Burkill, 1985 ; Dalziel, 1937 ; Watt et Breyer-Brandwinjk, 1962). Le temps de rétablissement des groupes de chimpanzés est de 20 à 24 heures après mastication de la moelle amère. Ce temps est comparable à celui des populations locales de Tanzanie, qui utilisent une préparation froide, obtenue à partir de cette plante, pour traiter les parasitoses, diarrhées et troubles d'estomac (Huffman et al., 1993).

D'autres espèces végétales utilisées de la même manière par les chimpanzés à Gombé, Kahuei-biega et Tai sont connues pour être des plantes possédant des propriétés pharmacologiques. *V. colorata* et *V. amygdalina* sont deux espèces très proches. Les tradipraticiens arrivent difficilement à les reconnaître, cependant toutes les deux sont utilisées en ethnopharmacologie (Burkill, 1985). Des alcaloïdes, identifiés dans la moelle, la fleur et les feuilles de *V. hochstetteri* (Smolenski, Silinis et Farnsworth, 1974) peuvent posséder quelques activités biologiques. *P. hirsuta* et *E. macrocarpa* sont utilisées en Afrique de l'ouest pour traiter les troubles d'estomac et les coliques, comme antiseptique et analgésique, ou dans les maladies vénériennes (Abbiw, 1990). Une activité molluscicide a été aussi rapportée pour *P. hirsuta* (Okunji et Iwu, 1988).

L'étude phytochimique d'échantillons de *V. amygdalina* ramassés au Mahale (en 1989 et 1991), parmi les plantes utilisées par les chimpanzés, montre la présence de deux principales classes de composés bioactifs. A ce jour, 4 lactones sesquiterpéniques (Vernodaline, vernolide, hydroxyver-

nolide, vernodalol), 7 nouveaux saponosides stéroïdiques de type stigmastane (Vernonioside A1 à A4, B1 à B3), 2 aglycones correspondant à ces hétérosides (Vernoniol A1 et B1) ont été isolés (Okunji et Iwu, 1988 ; Jisaka et al., 1992 a et b, 1993 a et b). Les lactones sesquiterpéniques se trouvent dans les différentes espèces de *Vernonia*. Ces composés sont le support d'activités anthelminthique, antiamibienne, antitumorale et antimicrobienne (Jisaka et al, 1992 a et b, 1993 a ; Asaka, Kubota et Kulkarni, 1977 ; Gasquet et al., 1985 ; Kupchan et al., 1969 ; Toubiana et Gaudemer, 1967). D'après Koshimizu et al. (1993), l'extrait méthanolique des feuilles inhibe la promotion des tumeurs et possède une activité immunosuppressive.

L'activité antischistosomiale in vitro a été observée avec les composants majoritaires : le vernonioside B1 (saponosides stéroïdique) et la vernodaline (lactone sesquiterpénique). Les deux composés agissent en inhibant la mobilité des parasites adultes et la capacité de ponte des femelles (Jisaka et al., 1992 b). Ces résultats confirment la diminution du nombre de vers nodulaires dans les fécès des chimpanzés après la mastication du *V. Amygdalina*, observée 20 heures après l'utilisation de la plante (Huffman et al., 1993).

In vivo, chez la souris infestée par des schistosomes, la vernodaline est la plus active. La dose létale pour les vers varie selon la voie d'administration : 5 mg par souris par voie orale (pour un poids moyen de 40 gr.), 2 mg par injection IP ou 5 mg/souris par voie sous-cutanée ou intramusculaire (Jisaka et al., 1992 b). La vernodaline par voie orale à 2,5 mg/souris n'a pas d'effet alors que le praziquantel agit à 2,5 mg (Ohigashi et al., 1994).

La vernodaline, composé très toxique, est abondante dans les feuilles et les écorces, et se trouve en très faible quantité dans la moelle. Ceci peut expliquer le fait que les chimpanzés ne consomment pas les feuilles et les écorces, mais plutôt la moelle qui est plus riche en hétérosides stéroïdiques (Jisaka et al., 1992 a ; Ohigashi et al., 1994).

Tous les composés isolés de *V. amygdalina* ont été également testés, in vitro, sur *Leishmania infantum*, *Entamoeba histolytica*, une souche multirésistante de *Plasmodium falciparum* (Ohigashi et al., 1994). L'activité antipaludique des lactones sesquiterpéniques était significative, cependant les CI_{50} obtenues étaient 20 fois plus élevées que la chloroquine diphosphatée (Ohigashi et al., 1994). Les hétérosides stéroïdiques ont montré une plus faible activité antipaludique, cependant leur aglycone était très actif sur le Plasmodium et l'amibe, notamment le vernoniol A4 (Ohigashi et al., 1994).

L'ingurgitation des feuilles

Il n'y a jusqu'à présent aucune preuve directe en faveur d'une action chimique des feuilles avalées sur l'expulsion des vers. On peut imaginer que l'action chimique des feuilles avalées serait de diminuer la capacité des vers à s'attacher solidement à la muqueuse intestinale ; ce qui les prédisposerait à être entraînés par ces mêmes feuilles pliées et rugueuses à travers la lumière intestinale et d'être éliminés (Huffman et al., 1996). Récemment, nous avons étudié in vitro les activités antischistosomiales et antipaludiques de 5 plantes appartenant à différentes familles botaniques. Les feuilles de ces plantes sont ingurgitées par les singes dans 5 sites d'étude : il s'agit de *Maniophyton fulvum* Mull. Arg. (Euphorbiaceae), *Ipomea involucrata* P. Beauv. (Convolvulaceae), *T. orientalis*, *Lippia plicata* Baker (Verbenaceae) et *Lagenaria abyssinica* (Hook.f.) C. Jeffrey (Cucurbitaceae) (Huffman et al., sous presse). Sur les extraits de 5 plantes testées, 4 ont manifesté, à 100 mg/ml, une activité inhibitrice de la ponte des schistosomes adultes. Ces extraits sont aussi actifs sur le plasmodium. L'isolement et l'identification des composés actifs sont en cours. Ces résultats montrent que les feuilles avalées agissent aussi par une action chimique.

Ces observations ont été renforcées par d'autres études in vitro sur l'activité antimicrobienne de 5 plantes dont les feuilles sont ingurgitées par des chimpanzés. Les extraits de ces feuilles ont été testés sur 3 souches de bactéries G+, 4 souches de bactéries G- et 1 souche de levures pathogènes. Les extraits de *Lippia plicata* et *T. orientalis* inhibent la croissance de *Staphylococcus aureus* et *Escherichia coli*. L'extrait de *L. plicata* était aussi actif sur une souche de *Pseudomonas aeruginosa* (Huffman et al., sous presse).

FUTURES ORIENTATIONS ET APPLICATIONS PRATIQUES

Les observations décrites dans cet article suggèrent l'existence d'une adaptation de comportement qui permet aux anthropoïdes de contrôler leurs affections parasitaires. Ces éléments sont en faveur d'une automédication, ce qui est démontré par la modification du taux d'infestation suite à la consommation occasionnelle de certaines plantes. Ce modèle peut être appliqué à d'autres primates qui subissent des infections parasitaires saisonnières. Mais d'autres influences peuvent être à l'oeuvre, et cette possibilité ne devrait pas être ignorée.

La surveillance systématique individuelle (et non des populations) du taux d'infestation tout au long de l'année est un moyen efficace pour identifier les parasites prédominants, ainsi que la période correspondant aux pics d'infestation (Huffman et al., 1997). Une surveillance étroite et à long terme de l'état de santé des différents membres du groupe doit être faite en analysant en détail la répartition de leur activité (temps de repos, temps de repas, locomotion, etc.), et en recherchant de manière systématique des signes de changement de l'état général (ex. diarrhée, toux, écoulement nasal, etc.). Cette surveillance permet de détecter et d'identifier les maladies qui surviennent, d'analyser leurs conséquences sur l'individu, et de comprendre le fonctionnement et l'efficacité de l'automédication.

Les parasitoses intestinales ne sont pas les seules causes de maladie. Pour identifier les autres causes, la capture des animaux et leur détention pour faire des prélèvements sanguins et tissulaires, présentent de grandes difficultés ce qui nécessiterait la mise au point d'autres techniques pour les contourner.

D'autre part, il faut développer des collaborations entre chercheurs de différentes disciplines (vétérinaires, médecins, pharmacologues, phytochimistes, etc.) pour arriver à comprendre les implications de l'automédication. La recherche multidisciplinaire conduite au parc de Mahale par le CHIMPP group (Chemo-ethnology of Hominoid interactions with medicinal plants and parasites) est un exemple de ce type de collaboration (voir Huffman, 1993 ; Jacobsen et Hamel, 1996).

Trois des plus grandes contraintes rencontrées sur le terrain lors de l'étude du comportement lié à l'automédication sont : (1) l'impossibilité de prédire l'occurrence des comportements, (2) la difficulté à suivre et observer les animaux malades en permanence, et (3) les contraintes dues aux travaux expérimentaux.

Il est souhaitable de surmonter ces contraintes afin de vérifier les hypothèses proposées dans le domaine de l'automédication. On peut, par exemple, introduire des plantes médicinales dans les lieux où les groupes sociaux de primates vivent en captivité, ce qui permettra d'évaluer les critères de sélection de ces plantes par les primates, et de savoir comment l'acquisition est faite puis transmise dans le groupe. Une telle application dans les zoos peut être d'une grande utilité pour le développement de nos connaissances et pour la santé des animaux capturés.

Plantes médicinales et enrichissement de l'environnement dans les zoos

Depuis 1985, un projet original sur l'apport des plantes médicinales chez les primates en captivité a été entrepris dans le zoo d'Apenheul en Hollande (Vermeer, 1995). Dans un premier temps, il a fallu détecter les causes majeures de problèmes de santé dans une population de singes laineux (*Lagothrix lagoticha*) vivant dans ce zoo. Ensuite, des plantes médicinales ont été plantées sur des parcelles de terrains, puis couvertes par des treillis en fil de fer. La hauteur du filet était choisie de manière à permettre à la population de singes d'avoir accès aux plantes, tout en les empêchant de les détruire complètement.

Parmi les plantes utilisées par ces singes, on trouve des espèces connues pour leur action antistress comme la camomille, *Matricaria chamomilla* (Linn.) (Compositeae), Catnip *Nepeta cataria* (Linn.) (Labiateae), la lavande *Lavendula angustifolia* (Labiateae), des espèces utilisées dans l'hypertension comme l'ail, *Allium sativum* (Linn.) (Liliaceae), l'aubépine, *Crataegus oxyacantha* (Linn.) (Rosaceae), et des espèces actives sur les infections de la vessie comme *Berberis vulgaris* (Linn.) (Berberidaceae), le fenouil *Foeniculum vulgare* Gaertn. (Ombellifères). L'effet de ces plantes sur la santé de ces singes n'a pas été encore cliniquement évalué.

Un projet similaire a démarré dans le zoo de Denver au Colorado, en 1996, sous la direction de Merle Moore (administrateur responsable du programme et de la maintenance du paysage et de l'horticulture). Dans ce cas là, il s'agit de gorilles et d'orang-outangs.

Ces deux programmes font appel à des méthodes innovantes permettant aux animaux le libre choix de leur nourriture, tout en apportant un enrichissement environnemental dans les zoos (Vermeer, 1995). D'autres études doivent être encouragées, notamment pour déterminer les plantes à utiliser dans les zoos des pays en voie de développement.

Ressources médicinales pour le bétail des pays en voie de développement

Une des applications possibles des recherches sur l'automédication des singes anthropoïdes concerne l'utilisation de plantes en médecine humaine et vétérinaire. Les infections dues aux espèces d'*Oesophagostomum* sont communes aux primates, aux porcs, aux moutons, au bétail. Ces parasites, qui peuvent même infecter l'homme, sont considérés comme des agents pathogènes conséquents (voir Anderson, 1992 ; Brack, 1987 ; Polderman et

al., 1991). Des produits anthelminthiques à large spectre pour le traitement du bétail sont actuellement sur le marché. Cependant, la croissance de la résistance chimique à ces anthelminthiques et leur prix prohibitif font que leur utilisation est presque impossible par les propriétaires de bétail ruraux et les parcs zoologiques dans les pays africains en voie de développement (Jackson, 1993 ; Mathias et al., 1996 ; Roepstorff, Bjørn et Nansen, 1987).

Récemment, un grand intérêt s'est manifesté pour l'emploi en thérapeutique des produits naturels provenant des plantes utilisées en ethnomédecine (cf. Kasonia et Ansay, 1994 ; McCorkle, Mathias et Schillhorn van Veen, 1996 ; Bøgh, Andreassen et Lemmich, 1996). L'étude de l'automédication chez les grands singes peut être aussi à l'origine de sources de produits naturels pour le traitement des parasitoses chez les hommes et chez les animaux domestiques et en captivité (Berry, McFarren et Rodriguez 1995). Sur la base des résultats obtenus dans le parc national de Mahale, un projet commun entre deux des auteurs de cet article (M.A.H. et P.N.), l'Université de Dar al Salam (Tanzanie), et l'Université d'Agriculture de Sakanii (Morogoro, Tanzanie) est actuellement en cours, afin de déterminer in vitro l'efficacité de ces plantes sur les infections à *Oesophogostomum* chez le porc.

Perspectives

Les recherches sur le comportement lié à l'automédication chez d'autres espèces de primates doivent être encouragées. Comme il a été démontré dans cet article, les réponses aux quelques questions posées conduisent à d'autres interrogations. De plus en plus de chercheurs s'intéressent à l'étude de l'automédication, ce qui apportera de plus en plus de réponses aux questions posées. Il est important de découvrir les causes qui menacent directement la santé et la survie d'un groupe de population, et de connaître leurs propres moyens d'automédication. Ainsi, l'utilisation de l'argile pour éliminer les composants toxiques des plantes riches en métabolites secondaires est considérée comme un moyen qui a permis l'élargissement de la gamme des plantes alimentaires depuis nos ancêtres préhominidés jusqu'à notre époque, et plus particulièrement pendant certaines périodes critiques de l'année (Johns, 1990). Le fait que différentes populations de chimpanzés et les humains sélectionnent parfois les mêmes plantes pour soigner les mêmes causes ou maladies suggère que les comportements d'automédication sont inscrits de longue date dans la phylogénèse. On peut penser que nos ancêtres hominidés utilisaient des critères similaires à ceux des singes

et des hommes de notre époque pour sélectionner les plantes biologiquement actives. Certes, nous ne possédons pas de preuves provenant des études des fossiles, mais cette hypothèse est probable, compte tenu des similitudes que nous avons observées entre les comportements d'automédication de l'homme et ceux du chimpanzé.

Quoi qu'il en soit de l'ingestion par les chimpanzés de certaines plantes afin d'expulser certains parasites saisonniers, ou de l'influence du régime alimentaire ou du climat sur la période de fécondité chez les femelles vervet (Whitten, 1983), nous ne pouvons pas nier la complexité de des interactions entre primates, parasites et plantes. L'étude de ces interactions est originale et difficile. Elle donne une dimension nouvelle à l'étude du comportement écologique des primates.

ABSTRACT

The study of self-medication in non-human primates sheds new light on the complex interactions of animal, plant and parasite. Investigation into the chemical ecology of the great ape diet have begun to broaden our understanding of the possible preventative affects of the natural plant diet against disease. A variety of non-nutritional plant secondary compounds and nutrient-poor bark are found in the primate diet, but little is yet known about the possible medicinal consequences of their ingestion. The great apes are largely frugivorous but also consume the leaves, pith, seeds, flowers, bark and sap of many species. A variety of interesting secondary compounds, including tannins, saponins, alkaloids, terpenes, and glycosides have been isolated from some of these plants. Pharmacological and ethnomedicinal sources indicate a wide range of biological properties such as antischistosomal, antimalarial, antiviral, antibacterial and antifungal activity. While these compounds are considered to be a plant's front line defense against all but the most specialized herbivores, great apes have incorporated them into their diet. Recent studies of the African great ape support a hypothesis in progress (Huffman, 1997) that the non-nutritional ingestion of certain plant species aid in the control of parasite infection and provide relief from related gastrointestinal upsets. Parasites can cause a variety of diseases which affect the overall behavior and reproductive fitness of an individual. Therefore the need to counteract such pressure should be great. The effects of parasitosis on the host and the host's response to infection is undoubtedly the product of a long evolutionary process. Detailed behavioral, pharmacological and parasitological investigations of two proposed

anti-parasite behaviors, bitter pith chewing and leaf swallowing, have been conducted on three East African chimpanzee populations (Mahale, Gombe, Kibale), but are now known to occur at 11 sites across Africa among chimpanzees (all subspecies) including bonobos, and lowland gorillas. A third wide spread behavior under investigation for its possible self-medicative value is geophagy. The hypothesis that bitter pith chewing has medicinal value for chimpanzees was first proposed from detailed behavioral observations of patently ill chimpanzees ingesting *Vernonia amygdalina* Del. (Asteraceae) and later from parasitological and phytochemical analyses at Mahale. In two closely monitored cases of bitter pith chewing in sick individuals, recovery was noted within 20-24 hr. In one case the eggs per gram feces level of a nodular worm infection was also found to have dropped within 24 hr. Phytochemical analysis of *V. amygdalina* samples collected at Mahale revealed the presence of two major classes of bioactive compounds; 4 known sesquiterpene lactones, 7 new stigmastane-type steroid glucosides and 2 freely occurring aglycones of these glucosides. Some of the bioactive properties noted for these compounds isolated from *V. amygdalina* thus far include antischistosomal, plasmodicidal, amoebicidal, inhibition of tumor promotion and immunosupressive activities. Leaf swallowing involves folding rough, bristly leaves inside the mouth and swallowing them whole without chewing. The behavior is currently proposed to control strongyle nematode infection and relieve pain caused by tapeworm infection via the expulsion of these intestinal parasites. A significant relationship is recognized between leaf swallowing and the expulsion of nodular worms and tapeworms at Mahale and Kibale, respectively. At present there is no direct evidence from field observations to suggest a specific role for plant secondary compounds in parasite expulsion via leaf swallowing, but one way that nematode expulsion may be chemically mediated is by decreasing a worm's ability to attach itself to the mucosal wall of the intestine, making it more prone to being "swept out" by the same rough whole leaves as they pass through the gut. Support for some biological activity comes from recent analyses of five species swallowed by apes at five study sites. Crude extracts of four of the five species exhibit inhibition of egg-laying activity on adult schistosomes and weak plasmodicidal activity. Geophagy is commonly practiced by the great apes, humans and many other herbivorous animal species world-wide. The soils ingested are typically clay. Clay contains none of the essential components of nutrition; protein, carbohydrates, lipids, and vitamins. These fine grained mineral deposits consist mainly of the hydrous silicates of aluminum magnesium and or iron. The chief groups of clay minerals are kaolinite, halloysite,

illite, montmorillonite, and vermiculie whose outstanding property is the capacity for holding water. Geochemical and behavioral ecology studies of the mountain gorilla, chimpanzee and rhesus monkey suggests that they may ingest soil for rare minerals of possible nutritional value or to relieve diarrhea caused by dietary changes or parasite infection. All clay soils analyzed thus far have been shown to have components closely resembling those of Kaopectate, a pharmaceutical commercially sold to treat gastrointestinal upset and other intestinal aliments. From the ethnographic literature, clay is reportedly consumed for its effectiveness as an anti-diarrheal and prevention of stomach aches or vomiting. Observations that the same medicinal plants are selected or similar behavioral practices exhibited by apes and humans with similar illnesses, provide insight into the evolution of medicinal behavior in humans. The study of self-medication in great apes is expected to provide significant insights into the effective treatment of parasitosis in humans and captive animals. Increased collaboration between colleagues from the applied sciences is essential to fully understand the implications of these proposed self-medicative behaviors.

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AAVP Newsletter

American Association of Veterinary Parasitologists

June, 1998 Volume 20, Number 2

FROM THE SECRETARY/TREASURER

The 43rd Annual Meeting of the AAVP is fast approaching. Almost 100 people are pre-registered for the conference (as of 15 May), with the pre-registration deadline of 15 June. Most of the AAVP functions, except for Monday evening's social event and the President's AVMA/AAVP joint Symposium, will be held in the Renaissance Harborplace Hotel, 202 East Pratt Street, in Baltimore ((410) 547-1200. This location is a prime spot on the newly renovated Inner Harbor, a few blocks from the Baltimore Aquarium, Maryland Science Center, shopping, B&O Train Museum and other attractions. Rob Rew has assembled a great program, starting with the first session at 3PM Saturday afternoon and ending Tuesday noon with Jimmy Williams's President's Symposium. In between, there are plenary sessions, abstracts, THREE company-sponsored socials plus coffee and rolls every morning. Overviews of the program titles together with the meeting room assignments are listed elsewhere in the Newsletter. In addition, if you asked to be notified about the acceptance of your abstract, you should have received a notice from Dr. Rew by now. If you haven't already done so, make your travel arrangements to not miss a minute. Notice of pre-registration postcards will be sent 17 June 1998. Please bring the card as your evidence of registration. If you need to know whether your registration was received prior to that date, call, fax or e-mail the numbers below. The on-site staff in Baltimore will provide you with badges, Proceedings and other meeting material. If you do not take advantage of pre-registration, you will be able to register starting at 2PM Saturday and all day Sunday on site. There will be a registration area just outside of the AAVP meeting rooms in the Renaissance Harborplace Hotel. You can also check on the status of your dues and catch up, if necessary, at that time. We will also have a few exhibits in the registration area, so stop by and peruse the literature on display. If you didn't get a hotel reservation in the Renaissance, the AVMA will run a shuttle service among the various hotels and the convention center starting Sunday morning, which we are free to use. For those unable to attend the Baltimore meeting, Proceedings will be mailed to you immediately after the meeting. I look forward to seeing many of you in Baltimore.

This is my last Newsletter as your Secretary/ Treasurer. The AAVP Constitution wisely imposes term limits on the job, so someone new will hound you from these pages in the future. I would like to thank so many of you for the help and advice you have graciously offered over the last six years. The duties of Secretary/Treasurer have been enjoyable and a valuable opportunity to serve the

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the bullets for each parasite? What is missing from the current edition? Are there format changes that would make the book more useful?

I welcome your ideas on any aspect of this publication. Feel free to call or email me. I will be attending the annual meeting in Baltimore and will be soliciting opinions there as well. Of course, soon I will be badgering you for photographs again, but since we can use color slides for this edition I am hopeful that collecting the photos will be much easier this time around. Thanks in advance for your help and insight. *Submitted by Anne Zajac*, phone 540-231-7017, e-mail: azajac@vt.edu. □

Research News

Control of nematode infections by African great apes: A new paradigm for treating parasite infection with natural medicines?

Parasites cause a variety of diseases which can affect the overall behavior and reproductive fitness of the host making the need to counteract such pressure great. The effects of parasitosis on the host and the host's response to infection is thought to be the product of a long evolutionary process. Ecologist, Dan Janzen (1978), first suggested that the incidental ingestion of secondary plant compound rich plants by animals may help to combat parasites. Recent evidence from the African great apes suggest that certain plants are ingested perhaps directly for their antiparasitic properties (cf. Huffman, 1997). Unquestionably, the implications of self-medicative behavior in animals is of extreme interest when considering the evolution of host-parasite relationships. Such studies may also prove to be invaluable when looking for new avenues of treating parasite infections in humans and other animals. The purpose of this brief report is to describe cutting-edge developments in our knowledge of self-medication in the chimpanzee, present a primate based paradigm of parasite control, and to stimulate collaborative research into the practical application of this knowledge in the veterinary sciences.

The hypothesis currently being developed from the author's long-term collaborative investigation of wild chimpanzees is that these behaviors aid in the control of intestinal parasite infection and provide relief from related gastrointestinal upset (cf. Huffman et al., 1996; Huffman et al., 1993; Wrangham, 1995). Two types of self-medicative behavior, bitter pith chewing and leaf swallowing, have been documented in the greatest detail from studies of wild chimpanzees in the Mahale Mountains in western Tanzania. This discussion will focus largely on the work done by the author in Tanzania but the reader is referred to a recent review of the topic for further details (Huffman, 1997).

Bitter pith chewing

The hypothesis that bitter pith chewing has medicinal value for wild chimpanzees was first proposed from detailed behavioral observations of patently ill chimpanzees ingesting Vernonia amygdalina Del. (Compositae) and from follow up parasitological and phytochemical analyses. When ingesting the young shoots of V. amygdalina, chimpanzees meticulously remove the outer bark and leaves to chew on the exposed pith, from which they extract the extremely bitter juice. Despite year round availability of the plant, use by chimpanzees is rare and occurs mainly during the early rainy season. Chewing of the bitter pith of two other Vernonia species by chimpanzees has been observed at Gombe, Tanzania and Kahuzi-Biega, former Zaire. Another two species from two genera are also known to be ingested by chimpanzees in the Tai forest, Ivory Coast.

Leaf swallowing

Leaf swallowing behavior was first reported for chimpanzees in east Africa at Gombe and Mahale (Wrangham & Nishida, 1983). Like bitter pith chewing, despite year round availability of these plants, use by chimpanzees at Mahale and Gombe is rare and occurs mainly during the early to mid-rainy season. Currently, leaf swallowing behavior involving 30 different plant species has been observed in 9 populations of the three chimpanzee sub-species and in one each of bonobo and the eastern lowland gorilla at 10 sites across Africa. Leaf swallowing is unlikely to provided any nutritional value because the undigested leaves are expelled whole in the dung. The plant species used vary in life form (herb, vine, shrub, tree), but the common property linking all of these plants is their hairy,

rough-surfaced leaves. The distal half of each leaf is selected one at a time, folded by tongue and palate as they are slowly pulled into the mouth and then individually swallowed whole. An individual may swallow anywhere from one to 100 leaves in one bout.

Typically, nearby chimpanzees do not join in and chew bitter piths or swallow whole leaves, unlike a group of foraging individuals converging upon a food source. Infants between 1-3 years of age, however, have been observed on occasion to taste a piece of discarded pith or to fold and half-heartedly swallow the same rough leaves used by their ill mothers or other elder individuals. This suggests that aspects of both behaviors must be learned. The relative contributions of instinct and learning in the acquisition of self-medicative behavior is not yet well understood, but both are thought to be involved.

The evidence for ape self-medication and its proposed antiparasitic function

General detailed observations on the state of health at the time bitter pith was chewed or whole leaves were swallowed has verified ill health (diarrhea, constipation, malaise, nematode infection) in most individuals. Detailed observations of two individuals documented recovery within 20-24 hr. from a lack of appetite, malaise, and constipation or diarrhea after chewing V. amygdalina bitter pith (Huffman and Seifu, 1989; Huffman et al., 1993).

A longitudinal investigation of the intestinal parasite fauna of Mahale chimpanzees shows that they are infected by at least three parasite species from three genera of nematodes, *Strongyloides fulleborni*, *Trichuris trichiura*, and *Oesophagostomum stephanostomum*; 1 genus of trematode, *Dicrocelium lanceatum*; and 4 genera of protozoa, *Entamoeba coli*, *Endolimax nana*, *Iodamoeba buetschlii*, and *Giardia lamblia* (Huffman et al., 1997). Among all M group chimpanzees monitored over a four year period, a statistically significant rainy season increase in the incidence of infection was noted only for individuals infected by *O. stephanostomum*. Among all three nematode species detected, infections of *O. stephanostomum* (95% 14/15) were also associated significantly more frequently with bitter pith chewing and leaf swallowing, than either *T. trichiura* or *S. fulleborni*. In one case the EPG level of *O. stephanostomum* was found to have dropped from a count of 130 to 15 within 20 hours. No change occurred in this individual's concurrent infections by *T. trichiura* (Huffman et al., 1993). When compared to seven other individuals with *O. stephanostomum* infections monitored over the same period, this was the only case in which such a dramatic drop in EPG was noted. To the contrary, the overall tendency was for EPG's to rise at this time of the rainy season.

Across Africa, a concoction made from V. amygdalina is a traditionally prescribed treatment for malarial fever, schistosomiasis, amoebic dysentery, several other intestinal parasites and stomach upset (Huffman, Koshimizu, Ohigashi, 1996). Our phytochemical analysis of *V. amygdalina* samples collected from plants used by chimpanzees at Mahale have revealed the presence of two major classes of bioactive compounds, sesquiterpene lactones and the newly discovered stigmastane-type steroid glucosides (Ohigashi et al., 1994). The sesquiterpene lactones present in *V. amygdalina* are well known for their anthelmintic, antiamoebic, antitumor, and antibiotic properties. From both groups of compounds isolated from this species thus far, we have found inhibition of tumor promotion and immunosupressive activities, *in vitro* antischistosomal activity as well as leishmanicidal (*Leishmania infantum*), amebicidal (Entamoeba histolytica), and plasmodicidal (K1 multi-drug resistant *Plasmodium falciparum*) activities (Koshimizu et al., 1993; Ohigashi et al., 1994).

Initially, leaf swallowing was suggested to deliver a potent anthelminthic compound to the site of parasite infection (Rodriguez & Wrangham, 1993) Detailed field observations, the diversity of plant species now known to be used, and phytochemical studies, however, have failed to support this hypothesis (Huffman et al., 1996; Page et al., 1997). Currently, the major mechanism of leaf swallowing is considered to be the physical expulsio of parasites. A possible phytochemical component, however, has not been totally out ruled (Huffman et al., in press).

The mechanism for *O. stephanostomum* worm expulsion at Mahale has been preliminarily deduced from the examination of chimpanzee dung samples. The occurrence of worms in the dung is extremely rare (3.7% of 245), but when they are found, the probability that whole leaves too are present is significantly high (p= 0.0001). In one instance, two nodular worms were actually found firmly attached by the trichomes to the surface of a leaf as if by Velcro. At the time of expulsion in most cases, adult worms were found trapped within the folded leaves or free floating in loose fecal matter. All worms recovered thus far have been alive and motile up to several days thereafter (Huffman et al., 1996).

Based on micro- and macro-parasitological inspection, leaf swallowing was found to affect only *O. stephanostomum* infections. Furthermore, from the current evidence *O. stephanostomum* is the only parasite stimulus consistently associated with the occurrence of these two self-medicative behaviors at Mahale.

Following accidental ingestion, the infective stage larvae of *O. stephanostomum* penetrate the wall of the gut, develop, and molt twice to become adults. The prepatent period is roughly one month and infections are typically self-limiting. At Mahale, the peak period of elevated reinfection (i.e. peak in individual O.s. EPG counts) is manifested two months after the onset of the rainy season around December and January. This is also the peak time that Mahale chimpanzees swallow leaves, chew bitter pith, and expel worms most frequently. Adult worms leave the mucosa and migrate back to the lumen of the bowel. Adult worms in the lumen rarely cause pathology. However, some of the larvae remain encapsulated, perhaps by pre-munition, causing inflammation that leads to diarrhea and abdominal pain, and in severe cases, simulated appendicitis. This discomfort is hypothesized to be the stimulus for leaf swallowing (and bitter pith chewing) behavior (Huffman et al., 1996). Removal of adult worms from the lumen may thus induce the encapsulated larvae to mature and leave the tissue. By freeing these encapsulated larvae, pain may be lessened or alleviated all together. Prolonged leaf-swallowing and bitter pith chewing around the peak period of re-infection would be expected to suppress the worm burden to tolerable levels during the remaining rainy season peak of re-infection. In the late-rainy and dry season months, re-infection is limited, and incidences of *O. stephanostomum* infection are quite low.

It is of interest to note that in western Uganda at the Kibale and Budongo Forest sites, however, the expulsion of tapeworm (*Bertiella studeri*) proglottids is closely associated with leaf swallowing (Wrangham, 1995; Huffman, unpublished data). It seems that different parasite species induce the same behavioral response by chimpanzees and other apes in different habitats. Leaf swallowing is reminiscent of grass swallowing in domestic cats and dogs and their wild counterparts, a behavior which has surprisingly remained unstudied. Homologous behaviors have recently been described in such diverse species as the brown bear and snow goose. In these two species, grass swallowing has also been associated with the expulsion of tapeworms prior to hibernation and winter migration, respectively (Huffman, 1997). Further details of leaf and grass swallowing in relation to *Bertiella* infections are needed.

A new paradigm for the treatment of parasite infections and anthelminthic resistance?

Anthelminthic resistance is a serious problem for livestock management (Geerts & Dorny, 1995; Jackson, 1993; Roepstorff, Bjoern, Nansen, 1987) and resistance to drugs used in treating life threatening diseases such as schistosomiasis and malaria in humans is a global problem urgently in need of solutions (Brindly, 1994; Geerts et al., 1997; Kremsner et al., 1997). The widespread geographical occurrence and broad taxonomical representation of great ape species exhibiting leaf swallowing and bitter pith chewing behaviors suggests that these self-medicative behaviors represent a stable evolutionary response to parasite infection. Can the study of great ape self-medication offer new strategies for countering parasite chemoresistance?

According to Geerts et al. (1997) factors selecting for anthelmintic resistance are mass treatment, frequent use of the same class of drugs over long periods of time and under dosing.

Theoretically, therefore, the converse approach may help stem anthelminthic resistance. Geerts and others have recommended a three pronged approach to stem or control anthelminthic resistance in livestock and human as follows: I. minimize treatments, II. rotate or combine different chemotherapy's, and III. administer proper dosage.

Some of our findings closely support this approach. Bitter pith chewing and leaf swallowing are sometimes displayed by an individual on the same day and in combination may have a bimodal affect on parasite infections. The occurrence of bitter pith chewing and leaf swallowing during the first few months of the rainy season in effect minimizes treatment to the heaviest periods of infection. Chimpanzees, of course unknowingly, are doing this by responding to the discomfort of higher level infections. Instead of totally eradicating them each season, chimpanzees in affect may be maintaining infections at sub-clinical levels most of the year. The bimodal action of bitter pith chewing and leaf swallowing behavior may act effectively towards the control of *O. stephanostomum* infections by the combination of treatment types used and the complex chemotherapy employed. The pith of *V. amygdalina* alone contains at least 18 different bioactive constituents from two distinct classes of compounds.

Continued muliti-disciplinary studies of self-medicative behavior in great apes and indeed other animal species is necessary. Such research will no doubt provide new insight into systems of parasite control occurring in nature and may help in the development of an evolutionarily based paradigm for countering parasite chemoresistance and approaching parasite related diseases in general (cf. Ewald, 1994).

Future prospects and collaborative research

Three of the greatest constraints on field investigations of self-medicative behavior are; 1) the unpredictability of the behaviors' occurrence, 2) the unreliability of being able to consistently follow and observe sick individuals over the course of their illness, and 3) the constraints on experimental manipulation. To overcome these limitations, increased collaboration between fieldworkers and applied animal scientists is essential in any attempt to fully understand the implications of animal self-medicative behavior.

Recently, great interest has been directed toward ethnoveterinary research. This is a fast growing field looking for alternative ways of treatment using natural plant products derived from ethnomedicines (e.g., McCorkle, 1996; Boegh, Andreassen & Lemmich, 1996). As the forgoing discussion has suggested, the study of great ape self-medication holds the potential to provide novel insights into strategies for suppressing or slowing down the rate of acquisition of chemoresistance by parasites and to provide viable new natural products for the effective treatment of parasitosis.

Through the controlled introduction of medicinal plants to captive primates and other alternative animal models, investigations into the potential for self-medicative behavior in this way can be expected to greatly advance our understanding of host-parasite relationships in the wild and to provide important benefits to captive animals. Based on the results of work in progress at Mahale, a joint effort between The C.H.I.M.P.P. Group*, the Danish Centre for Experimental Parasitology (The Royal and Agriculture University, Denmark) and The University of Dar es Salaam (Tanzania) is underway to determine the *in vitro* efficacy of medicinal plants against *Oesophagostomum* infections in swine and other livestock. * C.H.I.M.P.P. is an acronym for Chemo-ethology of Hominid Interactions with Medicinal Plants and Parasites, and was established in 1989 by the author with co-founders Prof. Koichi Koshimizu and Hajime Ohigashi of Kyoto University. The group currently has on-going collaborations in 10 countries.

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Submitted by Michael A. Huffman, Section of Ecology, Department of Social Behavior and Ecology Primate Research Institute, Kyoto University Inuyama, Aichi 484 JAPAN, Tel. : (0568) 63-0567 ext. 332 Fax: (0568) 63-0085 / 63-0565 International call/fax + 81 (568) home page: http://jinrui.zool.kyoto-u.ac.jp/CHIMPP/ CHIMPP. Html. □

Nominations Committee Report

AAVP Election Results

The results of this year's AAVP election are in. Congratulations to the following individuals who were elected by the membership of AAVP for the following offices and committee assignments. **Vice President** - Tom Kennedy; **Secretary/ Treasurer** - Dan Snyder; **Nominating Committee** – Linda Mansfield and Al Marchiondo.

I wish to thank all AAVP members who sent in their ballots, and the other members of the Nominating Committee, Drs. Conder, Fayer, Klei, Lindsay, and Stromberg, for their work on this year's election. *Submitted by Kevin Kazacos.* □

International Journal for Parasitology 29 (1999) 1087–1091

Research note

Molecular separation of *Oesophagostomum stephanostomum* and *Oesophagostomum bifurcum* (Nematoda: Strongyloidea) from non-human primates

R.B. Gasser[a,*], W.G. Woods[a], M.A. Huffman[b], J. Blotkamp[c], A.M. Polderman[c]

[a]*Department of Veterinary Science, The University of Melbourne, Princes Highway, Werribee, Victoria 3030, Australia*
[b]*Section of Ecology, Primate Research Institute, Kyoto University, Kanrin, Inuyama, Aichi 484-8506, Japan*
[c]*Department of Parasitology, Faculty of Medicine, University of Leiden, P.O. Box 9605, 2300 RC Leiden, The Netherlands*

Received 27 January 1999; received in revised form 29 March 1999; accepted 29 March 1999

Abstract

The ITS-2 sequences for adult specimens of *Oesophagostomum stephanostomum* from the common chimpanzee and *Oesophagostomum bifurcum* from the Mona monkey were determined. For both species, the length and GC content of the ITS-2 sequences were 216 bp and 43%, respectively. While there was no unequivocal sequence difference among individual worms representing each of the two species, five (2.3%) interspecific nucleotide differences were detected. These differences were associated with the presence of unique restriction sites in the ITS-2 sequence of *O. stephanostomum* for multiple endonucleases of diagnostic value for the differentiation of the two taxa by restriction analysis. Pairwise comparisons of the ITS-2 sequences of *O. stephanostomum* and *O. bifurcum* with published ITS-2 sequences for five different congeners indicated that these species from the subgenus *Conoweberia* are closely related, in accordance with previous morphological studies.

Keywords: Nematoda; *Oesophagostomum stephanostomum*; *Oesophagostomum bifurcum*; Non-human primates; Second internal transcribed spacer (ITS-2)

The 'nodule worms' (*Oesophagostomum* spp.: Nematoda: Chabertiidae) are important parasites found in livestock, primates and humans [1]. They can cause serious clinical disease (oesophagostomiasis) in the host, resulting in the formation of granulomata, caseous lesions or abscesses around encysted larvae in the small and large intestinal walls [1, 2]. Oesophagostomiasis has been described as a frequent disease found in laboratory primates [3] and is a serious health threat, particularly when associated with overcrowding and stress (reviewed [1]). *Oesophagostomum bifurcum*, *Oesophagostomum stephanostomum* and *Oesophagostomum aculeatum* (subgenus *Conoweberia*) are considered the three main species in non-human primates and the same species have also been described in humans [1]. However, there is considerable controversy over their identity and systematics based on morphological characters [4, 5]. Moreover, it is not clear whether non-human primates act as a reservoir for human infections in endemic areas (reviewed in Refs. [1] and [2]).

DNA technology has provided useful tools for addressing taxonomic and epidemiological problems related to parasites. Recently, DNA sequencing has allowed genetic characterisation of five species of *Oesophagostomum* found in livestock by their second internal transcribed spacer (ITS-2) of rDNA [6]. The ITS-2 sequence provided reliable genetic markers for their specific identification, with low levels (<1%) of intraspecific sequence variation and interspecific differences ranging from 10 to 41% [6]. Another study demonstrates that ITS-2 also provides genetic markers for the identification of *O. bifurcum* in humans [7]. However, there are no sequence data available for specimens of *Oesophagostomum* derived from non-human primates. In this study, we have characterised the ITS-2 sequences of adult specimens of *O. stephanostomum* from the common chimpanzee (*Pan troglodytes*) and of *O. bifurcum* from the Mona monkey (*Cercopithecus mona*) and compared the sequences with those of other species within the subfamily Oesophagostominae.

Adult worms of *O. stephanostomum* ($n = 3$) were recovered from a chimpanzee in Tanzania (Mahale) and *O. bifurcum* ($n = 4$) from a Mona monkey in Ghana (Fiema). The worms were identified according to existing descriptions [4, 8], and genomic DNA was extracted from individual worms using an SDS/proteinase K (Boehringer Mannheim) isolation protocol [9]. The ITS-2 (plus flanking sequence) was amplified by PCR [10] in a 50 l reaction volume, heated at 95 C for 5 min for 1 cycle and then for 30 cycles at 95 C for 30 sec (denaturation), 55 C for 30 sec (annealing) and 72 C for 30 sec (extension), using the oligonucleotide primers NC1 (forward: 5 -ACGTCTGGTTCAGGGTTGTT-3) and NC2 (reverse: 5 -TTAGTTTCTTTTCCTCCGCT-3) [9] using appropriate controls. PCR products were detected on 2% agarose-TBE (65 mM Tris–HCl, 22.5 mM boric acid, 1.25 mM EDTA, pH 9) gels, purified over spin columns (Wizard PCR Prep, Promega) and subjected to cycle-sequencing using the *f*-mol kit (Promega) employing the same primers as for primary amplification. The ITS-2 sequences were aligned manually. Pairwise comparisons were made of the sequence differences between species (D) using the formula $D = 1\ (M/L)$, where M is the number of alignment positions where the two taxa have a base in common, and L is the number of alignment positions over which the two taxa are compared. Restriction mapping of the ITS-2 sequences for 58 common endonucleases was carried out using the MacVector program (Kodak), and PCR-restriction fragment length polymorphism (PCR–RFLP) was performed as described previously [11].

For both *O. stephanostomum* and *O. bifurcum*, the length and GC content of the ITS-2 sequences were 216 bp and 43%, respectively. Polymorphic sites in the sequences were detected at several nucleotide positions (Fig. 1), but there was no unequivocal sequence difference among individual worms representing each of the two species. Fig. 1 shows the alignment (over 216 positions) of the (consensus) ITS-2 sequences for *O. stephanostomum* and *O. bifurcum* from non-human primates with a previously published sequence for *O. bifurcum* from humans from Togo ([7]; accession no. Y11733). While there was no unequivocal sequence difference in the ITS-2 between *O. bifurcum* from humans and that from a monkey from Ghana, there were five (2.3%) nucleotide differences between the sequences of *O. stephanostomum* and *O. bifurcum*, which were attributable to transitions at nucleotide positions 28, 76 and 156, and transversions at positions 94 and 173 (see Fig. 1). Pairwise comparisons of the ITS-2 of *O. stephanostomum* and *O. bifurcum* with previously published ITS-2 sequences for five other species representing the subgenera *Oesophagostomum* (*O. dentatum* and *O. quadrispinulatum*), *Proteracrum* (*O. columbianum*), *Hysteracrum* (*O. venulosum*) and *Bosicola* (*O. radiatum*) [6] revealed differences ranging

Note: Nucleotide sequences reported in this paper are available in the GenBank database under the accession numbers AF136575 and AF136576.

* Corresponding author. Fax: +613-97410401; e-mail: r.gasser@vet.unimelb.edu.au

0020-7519/99/$20.00
PII: S0020-7519(99)00037-5

Fig. 1. Alignment of the second internal transcribed spacer (ITS-2) (consensus) sequences for *Oesophagostomum stephanostomum* (OSc) from the chimpanzee and *Oesophagostomum bifurcum* (OBm) from the Mona monkey with a previously published sequence for *O. bifurcum* (OBh) from humans [7]. Polymorphic positions are indicated by IUPAC codes (W = T/A, R = G/A, M = C/A, V = A/C/G, Y = C/T). An asterisk and a dot indicate a nucleotide difference among the sequences and a polymorphic position, respectively.

from 2.3 to 41% (Table 1). The sequence difference (2.3%) between *O. stephanostomum* and *O. bifurcum* was substantially lower than levels found among all other species (9.2–40.6%), indicating that this pair of species (subgenus *Conoweberia*) from primates are closely related, as previously proposed in morphological studies [4, 13]. Compared with the magnitude of genetic differences in ITS-2 sequences among other congeners, the absence of any nucleotide difference in ITS-2 sequence between the *O. bifurcum* specimens from humans and monkey (Fig. 1) provided some support for the hypothesis that they represent a single species. However, the alternative hypothesis that they represent different species cannot be ruled out, as it is possible that different species of helminth can have the same ITS-2 sequence [12].

The magnitude of sequence difference (2.3%) in the ITS-2 sequence between *O. stephanostomum* and *O. bifurcum* was greater than the degree of sequence variation detected within any of the species of *Oesophagostomum* examined so far (<1%) [6, 7], indicating that the interspecific nucleotide differences provide useful genetic markers for the delineation of these two taxa. These interspecific differences were associated with either the presence or the absence of restriction sites in the ITS-2 sequence for multiple endonucleases. In the ITS-2 of *O. stephanostomum*, unique recognition sites existed for endonucleases *Afl* III, *Bsp* W1, *Hga* I and *Nsp* I at nucleotide positions 91, 25, 34 and 95, respectively. Also in that sequence, two sites (positions 95 and 206) existed for endonuclease *Nla* III; whereas only the latter site was present in the ITS-2 sequence of *O. bifurcum*. *Nla* III was selected as an example to demonstrate the usefulness of PCR–RFLP of ITS-2 to separate *O. stephanostomum* and *O. bifurcum* (Fig. 2). Although some polymorphic nucleotide positions were detected in the sequences for the two species, they did not occur within any of the five endonuclease recognition sites, and should, therefore, be of no consequence in the specific identification of these parasites. Nonetheless, future work should assess the degree of ITS-2 sequence variation among a large number of individuals for each species derived from both non-human primates and humans from various geographical locations, and should include *O. aculeatum*, and any other species from primates when specimens become available. Given the difficulty in specifically identifying the eggs and larvae of *Oesophagostomum* spp. from faecal and environmental samples using morphological methods (c.f., Ref. [7]), the definition of genetic markers in the ITS-2 for *O. stephanostomum* and *O. bifurcum* has implications for the development of a DNA method for the specific diagnosis of oesophagostomiasis in primates, and for investigating its prevalence and transmission dynamics.

Table 1
Pairwise comparison of sequence differences (%) in the ITS-2 among seven species of Oesophagostominae

	Species	1	2	3	4	5	6	7
1	*Oesophagostomum radiatum*	–						
2	*Oesophagostomum venulosum*	40.6	–					
3	*Oesophagostomum dentatum*	24.1	30.9	–				
4	*Oesophagostomum quadrispinulatum*	18.0	34.8	12.0	–			
5	*Oesophagostomum columbianum*	24.7	30.1	11.9	14.2	–		
6	*Oesophagostomum bifurcum*	22.5	28.6	10.1	14.8	10.1	–	
7	*Oesophagostomum stephanostomum*	24.3	28.2	10.1	15.2	9.2	2.3	–

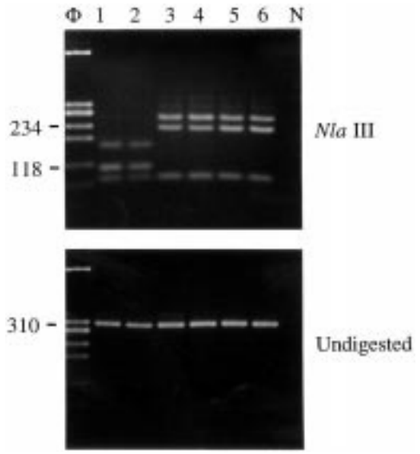

Fig. 2. Polymerase chain reaction–RFLP of the second internal transcribed spacer of rDNA of adult individuals of *Oesophagostomum stephanostomum* from the chimpanzee (lanes 1 and 2) and *Oesophagostomum bifurcum* from the Mona monkey (lanes 3 and 4) or from humans [7] (lanes 5 and 6) using the endonuclease *Nla* III. Undigested PCR product (310 bp). M represents the X174-*Hae* III marker (Promega) indicating sizes in bp, and N represents a no-DNA control.

Acknowledgements

The authors would like to thank P.A. Storey (Ministry of Health, Tamale, Ghana) for assisting in the collection of some samples, I. Beveridge for comments on the manuscript and X.Q. Zhu for assistance. Financial support to R.B.G. was provided by the Australian Research Council, the Department of Industry, Science and Tourism and the Collaborative Research Program (The University of Melbourne). Financial support to M.A.H. was provided by the Wellcome Trust and the Plant Sciences Research Foundation of the Faculty of Agriculture, Kyoto University.

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Journal of Tropical Ecology (1999) 15:565–588. With 5 figures

Chemistry, mineralogy and microbiology of termite mound soil eaten by the chimpanzees of the Mahale Mountains, Western Tanzania

WILLIAM C. MAHANEY*, JESSICA ZIPPIN*[1], MICHAEL W. MILNER*, KANDIAH SANMUGADAS*, R. G. V. HANCOCK†, SUSAN AUFREITER†, SEAN CAMPBELL‡, MICHAEL A. HUFFMAN¶, MICHAEL WINK#, DAVID MALLOCH$ *and* VOLLI KALM§

* *Geomorphology and Pedology Laboratory, Atkinson College, York University, 4700 Keele St., North York, Ontario, Canada, M3J 1P3*
† *SLOWPOKE Reactor Facility, Department of Pure and Applied Chemistry, University of Toronto, Toronto, Ontario, Canada*
‡ *Department of Geography, Arizona State University, Tempe, Arizona, U.S.A.*
¶ *Primate Research Institute, Section of Ecology, Kyoto University, Inuyama, Aichi, Japan*
\# *Institute of Pharmaceutical Biology, University of Heidelberg, Im Neuenheimer Feld 364, D-69120, Heidelberg, Germany*
$ *Department of Botany, University of Toronto, Toronto, Ontario, M5S 1A4, Canada*
§ *Institute of Geology, Tartu University, Tartu, Estonia*
(Accepted 27th March 1999)

ABSTRACT. Subsamples of termite mound soil used by chimpanzees for geophagy, and topsoil never ingested by them, from the forest floor in the Mahale Mountains National Park, Tanzania, were analysed to determine the possible stimulus or stimuli for geophagy. The ingested samples have a dominant clay texture equivalent to a claystone, whereas the control samples are predominantly sandy clay loam or sandy loam, which indicates that particle size plays a significant role in soil selection for this behaviour. One potential function of the clays is to bind and adsorb toxins. Although both termite mound and control samples have similar alkaloid-binding capacities, they are in every case very high, with the majority of the samples being above 80%. The clay size material (<2 μm) contains metahalloysite and halloysite, the latter a hydrated aluminosilicate ($Al_2Si_2O_4 \cdot nH_2O$), present in the majority of both the termite mound soil and control soil samples. Metahalloysite, one of the principal ingredients found in the pharmaceutical Kaopectate™, is used to treat minor gastric ailments in humans. The soils commonly ingested could also function as antacids, as over half had pH values between 7.2 and 8.6. The mean concentrations of the majority of elements measured were greater in the termite mound soils than in the control soils. The termite mound

[1] Corresponding author.

soils had more filamentous bacteria, whereas the control soils contained greater numbers of unicellular bacteria and fungi.

KEY WORDS: geophagy, soil ingestion, termite mound soil, toxin adsorption

INTRODUCTION

Geophagy has been observed in a diverse number of species throughout the world, such as mountain gorillas (Fossey 1983, Mahaney *et al.* 1990); colobus monkeys (Oates 1978); moustached tamarins (Heymann & Hartmann 1991); ungulates (Kreulen 1985, Mahaney *et al.* 1996a); elephants (Ruggiero & Fay 1994); Holstein cross cattle (Mahaney *et al.* 1996a); geese (Wink *et al.* 1993); and even humans (Aufreiter *et al.* 1997, Geissler *et al.* 1997, Johns & Duquette 1991, Vermeer 1966). Although the exact stimulus, or stimuli, for this behaviour in animals is not known it is suspected that these soils may offer nutritional benefits (Geissler *et al.* 1997, Johns & Duquette 1991, Kreulen 1985, Mahaney *et al.* 1990, Vermeer 1966) or have medicinal properties (Huffman 1997, Mahaney 1995a, 1996a, b) as they do for humans. Recently the possibility that primates incorporate non-nutritive, often toxic, chemical elements into their diet for treatment of disease has received wide attention (see Huffman 1997).

A number of scientists have repeatedly concluded that geophagy functions through: (1) adsorption of toxic plant compounds onto the surface of clay particles (Johns & Duquette 1991, Oates 1978, Wink *et al.* 1993), or absorption in the interlayer space of swelling clays (White & Hem 1983); (2) possible mineral supplementation (Davies & Baillie 1988, Heymann & Hartmann 1991, Hirabuki & Izawa 1990, Johns & Duquette 1991, Mahaney *et al.* 1990, Oates 1978); and (3) the clay minerals in the soil possibly alleviating stomach upset or relieving diarrhoea (Davies & Baillie 1988, Kreulen 1985, Mahaney *et al.* 1995b, Oates 1978).

Mahaney *et al.* (1996b) previously investigated the geochemistry and clay mineralogy of soil ingested from four termite mounds frequently utilized by chimpanzees in the Mahale Mountains National Park in Tanzania. They found that this soil could be a minor source of the nutritionally important elements, mainly iron and potassium. The clay mineralogy revealed a 4 : 1 ratio of metahalloysite/halloysite:smectite, a mineral combination similar to the active ingredients in the pharmaceutical Kaopectate™, which is used to treat minor gastric ailments in humans.

The present study examines the chemical, geochemical, mineralogical and biological properties of termite mound soil ingested by chimpanzees and soil from the forest floor that is not normally eaten to determine whether there is a stimulus or stimuli which might clarify the benefits of geophagy practised by chimpanzees of the Mahale Mountains.

METHODS AND MATERIALS

Study site

The study area is in the Mahale Mountains National Park in western Tanzania (latitude 6°S, 30°E) (Figure 1). This isolated mountain range extends

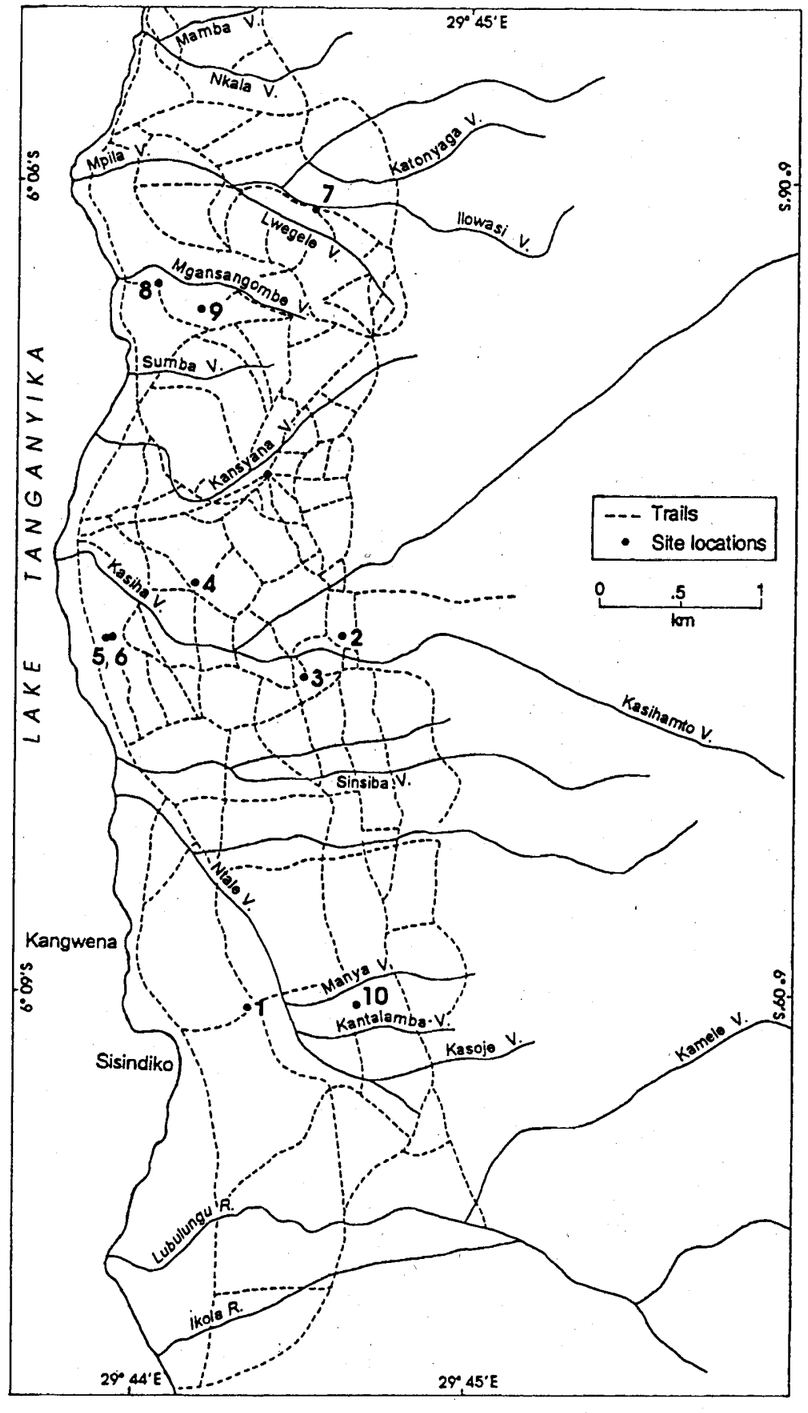


Figure 1. Location of geophagy sites in Mahale Mountains National Park, Tanzania.

north to south along the eastern shore of Lake Tanganyika and is characterized by extensive slopes and valleys, with the highest peak being Mt. Nkungwe at 2462 m asl.

The wet season begins in October and lasts until the beginning of May, with a short dry season from mid-January to February and a longer dry season from June to September (Takasaki *et al.* 1990). The mean annual rainfall is 1874.4 mm, the mean annual daily maximum and minimum temperatures are 29 °C and 18 °C, respectively (data taken from Kansyana camp, which is located within the study area). With high rainfall in the wet season (October–May), there is abundant moisture for soil weathering to occur.

The vegetation of the study site is characterized by semi-deciduous gallery forests which range from 780–1300 m above sea level. White (1983) has classified the vegetation zone as 'wetter Zambezian miombo woodland', dominated by *Brachystegia, Julbernardia* and *Isoberlinea* which extend over western Tanzania.

The Mahale Mountains lie within Ufipa terrane which contains basement rock consisting of coarse, crystalline metamorphic rock of sedimentary and volcanic origin. These include gneisses and schists, with biotite, but also contain kyanite, garnet, hornblende, graphite and chlorite; quartzites, crystalline marbles; amphibolites; pyroxenites, and charnockite rocks (Anon 1976). These may also provide minerals and/or release chemical elements to termite mounds.

Soils

The composition of the soil in the Mahale Mountains consists mainly of sandy clay loam with good drainage (Hathout 1972) and is of granitic–gneissic origin (Baker 1970). Because of the steepness of the terrain, most places in the Mahale Mountains appear to have relatively immature and stony soils (Collins & McGrew 1988). The organic horizons, where present, range between 0–2 cm (Collins & McGrew 1988); complete soil descriptions are not available but generalized horizon sequences indicate they are Inceptisols with A/B/C horizons in profile (Soil Survey Staff 1975).

In the first set of samples the termite mound soil colours range from yellowish brown (10YR 5/4, 6/6) to bright brown (7.5YR 5/6) and the control samples range from brown (10YR 4/4, 4/3) to dark brown (10YR 3/4, 3/3) (assessed using colour chips of Oyama & Takehara 1970). The second set of control sample colours are slightly darker; the termite mound soil colours range from brown (7.5YR 4/4) to dark brown (10YR 3/3, 3/4) and the control samples range from dark brown (10YR 3/3) to brownish black (10YR 2/2) (Oyama & Takehara 1970). The soil colours suggest chimpanzees are selecting soils with light brown colours and avoiding dark soils with higher organic matter content.

Within the study site area, termite mounds mainly *Macrotermes* and *Pseudocanthotermes* are ubiquitous. All members of a chimpanzee group, at any time of the day and throughout the year, can be observed ingesting clumps of termite mound soil *c.* 3 cm^3 in volume.

Analysis

The soils were collected in pairs with each pair consisting of a sample from a termite mound known to be frequently used by chimpanzees and a control sample taken from surrounding uneaten topsoil *c.* 5 m away from the termite mound. Neighbouring termite mound samples 5 and 6 share the same control sample. In data set 2, all of the samples were re-collected from the same termite mounds and forest floor from the first data set were used; when analysed the second sample set appeared to be different from the first set. Therefore, the two sample sets will be regarded separately and distinctly. The paired samples will be referred to below as 'tm' (termite mound) and 'c' (control) samples.

Particle size distributions were determined by a combination of sedimentation and wet and dry sieving (Day 1965). The sand fraction (63–2000 μm) was determined by wet sieving, with silt (2–63 μm) and clay (<2 μm) determined by hydrometer. An expanded description of this method is given in Mahaney (1990).

X-ray diffraction (XRD) was employed to identify and measure the relative abundance of primary and secondary minerals in the clay fraction. The clay fraction was agitated, centrifuged onto a ceramic tile, and then X-rayed on a Toshiba ADG-301H diffractometer with Ni-filtered CuKα radiation following methods outlined by Whittig (1965).

The fine fraction of the sand grains from 10 ingested samples (63–250 μm) was analysed to determine weathering states and composition of clay mineral coatings on the sands. This was accomplished using a JEOL JSM-840 scanning electron microscope (SEM) along with energy dispersive spectrometry (EDS).

Electron microprobe analysis was used to determine the elemental composition of the following soil samples: 5 and 6 c, 5 tm, 6 tm and 10 tm. For the purpose of this study the wavelength dispersive mode was used. The probe beam diameter was set to 5 μm and the probe current was 10 nA. The minimum detectability limits are shown on the top of Table 1.

The pH was determined by glass electrode, total soluble salt content by electrical conductivity (Bower & Wilcox 1965), and organic content by the Walkley-Black (1934) method. The concentrations of extractable cations (Na^+, Mg^{2+}, K^+ and Ca^{2+}) were measured using atomic absorption spectrophotometry (AAS) (McKeague 1976) and total Kjeldahl nitrogen by auto-analyser (AA) (Schuman *et al.* 1973).

The toxin adsorption capacities of soils in the first sample set were determined by capillary gas liquid chromatography using the alkaloids lupanine, sparteine, quinine and atropine. A mass of 100 mg of soil was dissolved in 5 ml distilled water; then 1000 or 5000 μg of alkaloids were added, the vials regularly shaken, and left for 30 min. After that time the flasks were centrifuged at 10,000 **g**, to pellet all soil particles. Then the supernatant was taken, alkaloids were extracted by solid phase extraction, and analysed quantitatively by

Table 1. Electron microprobe data from control samples 5 and 6, and termite mound samples 6, 10 and 5, from Mahale Mountains, Tanzania. Data are in percentages. Detection limits for each element are given on line 2. – means value below detectable limits.

Minimum limit to detection Point	Na_2O 0.013	MgO 0.01	Al_2O_3 0.014	SiO_2 0.014	P_2O_5 0.032	SO_3 0.027	K_2O 0.016	CaO 0.018	TiO_2 0.036	MnO 0.062	Fe_2O_3 0.06	BaO 0.086	Total
Transect 3–4, control sample 5 and 6; image 305, 190×													
	0.04	–	0.02	94.17	–	–	–	–	–	–	0.2	–	94.43
	0.18	0.18	15.1	35.02	0.25	0.07	5.76	0.11	0.2	–	1.76	0.12	58.75
	–	0.36	7.22	11.7	0.09	0.07	0.58	0.13	0.27	–	1.66	0.1	22.18
	0.05	0.05	13.91	41.1	–	–	0.61	0.06	0.2	–	1.4	–	57.38
		0.6	23.96	31.75	–	0.07	1.08	0.11	0.45	–	5.28	0.09	63.46
	0.08	0.4	23.09	28.35	0.14	–	0.78	0.11	0.37	–	4.66	–	57.98
	–	0.3	24.94	34.66	0.14	–	0.52	0.04	0.2	–	4.15	–	64.95
	0.05	0.43	22.98	27.98	0.27	–	0.81	0.07	0.67	–	5.93	0.1	59.19
	0.08	0.86	19.01	29.18	–	–	2	0.06	0.43	–	5.5	–	57.12
	0.13	0.73	22.41	29.1	0.05	0.05	1.11	0.03	0.4	–	4.65	0.17	58.83
Transect 5–6, mound sample 6; image 305, 190×													
	0.03	–	0.04	96.42	–	–	0.04	–	–	–	–	–	96.53
	0.24	0.78	18.54	25.46	0.05	–	0.63	–	0.32	0.26	15.1	–	61.38
	0.04	0.58	23.62	30.66	–	–	1.05	0.08	0.55	1.37	6.68	–	64.63
	–	0.65	19.44	23.9	0.21	–	0.83	0.06	0.5	0.87	14.7	–	61.16
	0.05	0.46	26	33.84	0.07	0.07	1.98	0.06	0.55	0.3	5.83	–	69.21
	0.07	0.71	28.55	35.79	0.11	–	1.31	0.1	0.57	0.1	7.72	–	75.03
	0.24	–	18.67	62.17	–	–	14.29	–	0.07	–	0.56	059	96.59
	0.53	–	12.55	37.55	–	–	5.18	–		–	0.46	022	56.49
	0.09	1.18	24.58	33.4	–	–	1.96	0.08	0.63	0.13	7.72	–	69.77
	0.42	–	16.61	61.49	–	–	13.55	–	–	–	0.24	0.5	92.81
Transect 7–8, mound sample 10; image 305, 300×													
	0.03	0.18	4.76	8.04	–	–	5.88	–	0.08	–	4.7	0.71	24.38
	0.11	0.75	32.48	28.07	–	–	6.02	–	0.07	–	4.03	0.58	72.11
	–	0.45	29.04	39.54	0.09	0.1	0.63	0.08	0.72	–	8.49	–	79.14
	0.07	0.32	29.7	34.19	–	–	0.54	0.11	0.92	–	8.62	0.1	74.57
	–	0.18	24.71	30.46	0.21	0.07	0.42	0.07	0.65	–	10.42	–	67.20
	0.18	0.3	29.17	37.4	0.25	–	0.65	0.2	0.8	–	8.39	–	77.34
	–	0.36	30.5	40.73	0.05	–	0.69	0.13	10.3	–	8.15	–	81.64
	0.03	0.25	31.37	39.86	0.25	0.07	0.6	0.1	0.83	–	7.19	–	80.55
	–	0.17	28.53	36.54	0.14	0.05	0.42	0.07	0.65	–	5.3	–	71.87
	0.07	0.33	24.36	30.68	–	–	0.67	0.1	0.75	–	13.2	–	70.16

Minimum limit to detection Point	Na_2O 0.013	MgO 0.01	Al_2O_3 0.014	SiO_2 0.014	P_2O_5 0.032	SO_3 0.027	K_2O 0.016	CaO 0.018	TiO_2 0.036	MnO 0.062	Fe_2O_3 0.06	BaO 0.086	Total
Transect 9–10, mound sample 10; image 305, 750×													
	4.25	0.08	14.1	26.12	–	0.15	6.42	0.28	0.43	–	6.65	–	58.48
	2.44	0.05	16.36	25.65	0.41	0.07	8.7	0.14	0.45	–	7.09	–	61.09
	1.15	0.15	18.35	30.49	0.11	–	1.47	0.1	0.6	–	6.66	–	59.08
	2.4	0.03	15.74	23.45	–	0.15	12.66	0.14	0.45	0.09	5.88	–	60.99
	4.04	0.2	17.06	29.25	0.09	0.2	2.48	0.27	0.47	–	5.73	–	59.79
	0.39	0.22	22.58	34.02	0.05	–	0.53	0.06	0.83	–	7.56	–	66.24
	0.05	0.27	20.95	34.17	0.16	–	0.57	0.07	0.68	–	8.21	–	65.13
	0.04	0.27	22.9	35.86	0.05	–	0.63	0.07	0.55	–	7.89	–	68.26
	0.08	0.27	21.37	34.87	0.11	–	0.59	0.06	0.85	–	6.98	–	65.18
	0.04	0.23	21.56	32.82	–	–	0.65	–	0.67	–	8.46	–	64.43
Transect 11–12, mound sample 5; image 305, 370×													
	–	0.81	16.76	31.17	0.07	–	1.14	0.18	0.48	–	5.46	–	56.07
	0.09	3.07	20.09	33.76	–	–	3.59	0.11	1.08	–	12.84	–	74.63
	–	0.46	26.55	36.95	0.07	–	1.02	0.2	0.85	–	7.55	–	73.65
	0.08	0.5	28.81	36.73	é	0.05	0.99	0.14	0.8	–	8.46	–	76.56
	–	0.23	8.65	83.65	0.14	–	0.69	0.04	0.23	0.1	2.1	–	95.83
	0.07	0.55	27.89	36.86	–	–	0.92	0.13	1.2	–	9.85	–	77.47
	0.07	0.63	24.64	45.1	–	–	1.24	0.11	1.22	0.14	6.76	–	79.91
	0.09	0.76	27.7	37.05	–	–	1.16	0.2	0.75	–	8.49	0.09	76.29
	–	0.32	21.88	55.07	–	–	0.87	0.1	0.32	–	4.53	–	83.00
	–	0.55	24.51	32.24	–	0.07	1.14	0.18	1.1	–	6.53	–	66.32

capillary gas liquid chromatography using authentic alkaloids as external standards (Wink 1993, Wink *et al.* 1995).

The geochemistry of the soils was accomplished using Instrumental Neutron Activation Analysis (INAA) at the SLOWPOKE Reactor Facility, University of Toronto. The concentration of the macro-, micro- and trace elements of the samples were measured using procedures established by Hancock (1984).

Dilution plating for microorganisms was carried out using a two-culture medium: modified Leonian's medium for fungi and nutrient agar for bacteria. One g of each sample was diluted serially to obtain dilutions of 1 : 10, 1 : 100, 1 : 1000, 1 : 10000 and 1 : 1000000. One ml of each dilution was pipetted into three Petri dishes containing cooled molten Leonian's and nutrient agar. The media were allowed to solidify and were incubated at 21 °C. After 7–10 d the colonies in each plate were counted and identified. The colony counts were multiplied by the dilution factor to calculate colony forming units (CFUs) per g of soil.

Standard χ^2 and t-test methods were used to establish the statistical significance of the termite mound vs. control soil data sets.

RESULTS

Particle size analysis

Particle size analysis was used to determine the relative proportion of sand, silt and clay for each soil sample. The majority of termite mound samples have a clay texture while the control samples are predominantly sandy clay loam as indicated by the ternary diagrams (Figures 2a, b). The data from the particle size curves for all termite mound samples show mean clay values of 45.8 ± 11.5%, sand values of 34.8 ± 8.6% and silt values of 19.4 ± 5.2%. The control samples show clay values of 28.5 ± 8.4%, sand values of 52.9 ± 8.4% and silt values of 18.6 ± 2.7%. The control samples fit well with the soil description given by Hathout (1972) for the area. However, the termite mound soil has a relatively greater clay content which arises from mound building activity.

Clay mineralogy

The clay material (<2 μm) was analysed and the results (Figure 3) show the presence of metahalloysite/halloysite, the latter a hydrated aluminosilicate ($Al_2Si_2O_4 \cdot nH_2O$), present in the majority of the termite mound and control samples. The first order reflection for metahalloysite, at 12.2° 2θ, disappears after heating to 500 °C (Brindley & Brown 1980), revealing that this clay is not kaolinite. Metahalloysite, an analog of purified kaolin clay, is the principal ingredient found in the pharmaceutical Kaopectate™, along with smectite, although at smaller concentrations. Smaller proportions of halloysite at different hydration states were also found in the samples. Approximately 60% of all samples contain illite/smectite. Other clay minerals identified were illite and kaolinite. Other primary minerals include quartz and orthoclase.

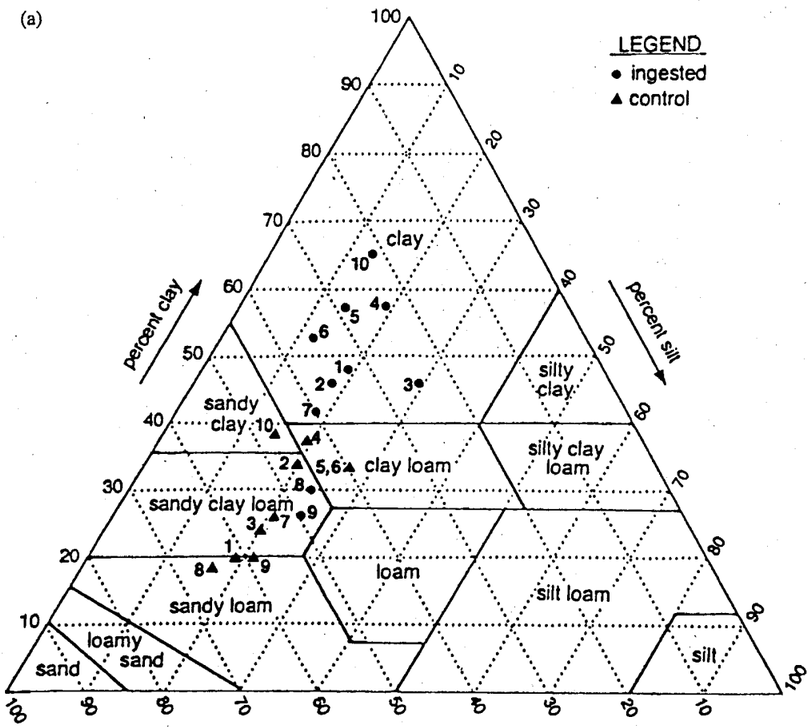


Figure 2. Soil textural classifications for sample sets (a) 1 and (b) 2. Ingested: termite mound soil.

As indicated by the reflections, there is very little difference in relative abundance of kaolinite and metahalloysite between the control samples and the ingested samples. This may be due to the fact that the uneaten samples are located close to the termite mounds resulting in some slope wash into the control samples.

Scanning electron microscopy

A representative cross-section of light and heavy minerals, examined by scanning electron microscope (SEM), from ingested samples 5, 6 and 9 and control samples 5 and 6 are shown in Figure 4. Hematite, an iron oxide, with a textured surface can be seen in Figure 4A. Epidote is shown to be highly weathered (Figure 4B) as well as having an etched surface (Figure 4C). A clay coating is evident on the centre of a quartz grain (Figure 4D). Figure 4E shows an orthoclase grain (left) surrounded by euhedral quartz grains possibly originating from a tuff. Minor etching and wear on the surface of an orthoclase grain is shown in Figure 4F. A phlogopite grain with platy structure and strong basal cleavage is shown in Figure 4G. A highly weathered iron oxide grain with a secondary iron coating is shown in Figure 4H.

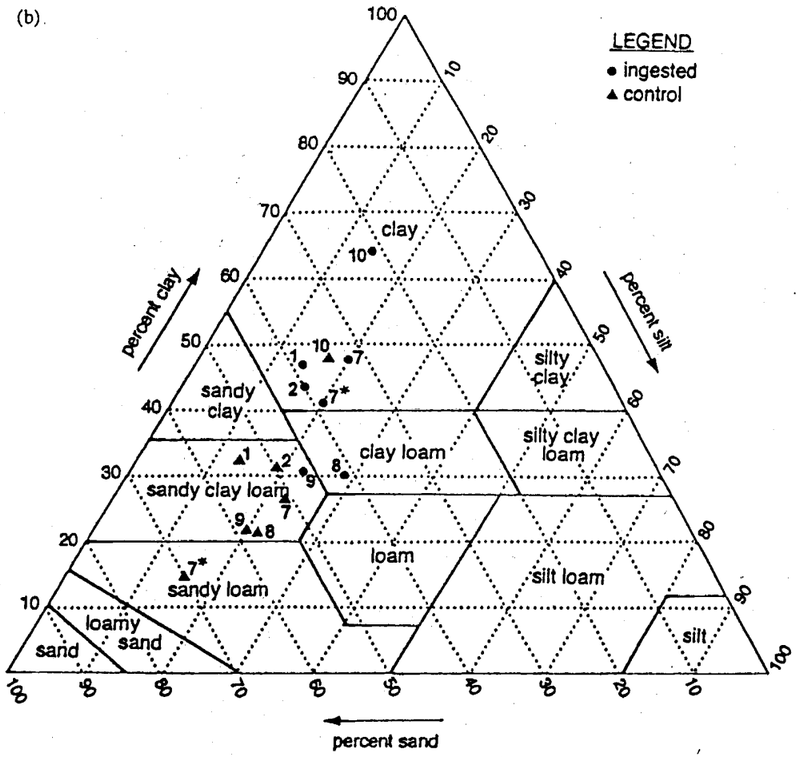


Figure 2 *continued.*

The cross-section of minerals examined by SEM illustrates that a great deal of weathering has taken place within the termite mound group of samples. Weathering may result in partial or full alteration of the primary mineral structure followed by release of nutritionally useful chemical elements such as K, Fe and Ca.

Electron microprobe

Electron microprobe combined with backscatter imagery was used to analyse samples 5 and 6 c, 5 tm, 6 tm and 10 tm. The transects from Table 1 are shown as black lines on the backscatter photographs (Figure 5). Nutritionally important elements that could potentially stimulate the practice of geophagy, such as Na, Ca, P, S, Mn and Mg, are quite low. The silica/aluminum ratio, is close to, but not consistently 1 : 1, which supports the 1 : 1 clay minerals reported herein. Iron (II), the element suspected as a possible stimulus by Mahaney *et al.* (1996a, b), does have concentrations that average 7.2% for 5 tm, 6.5% for 6 tm, and 7.8% for 10 tm. While the data overlap somewhat with the geochemistry reported below, the microprobe provides important information on P, S and Si, which are not obtainable with routine INAA.

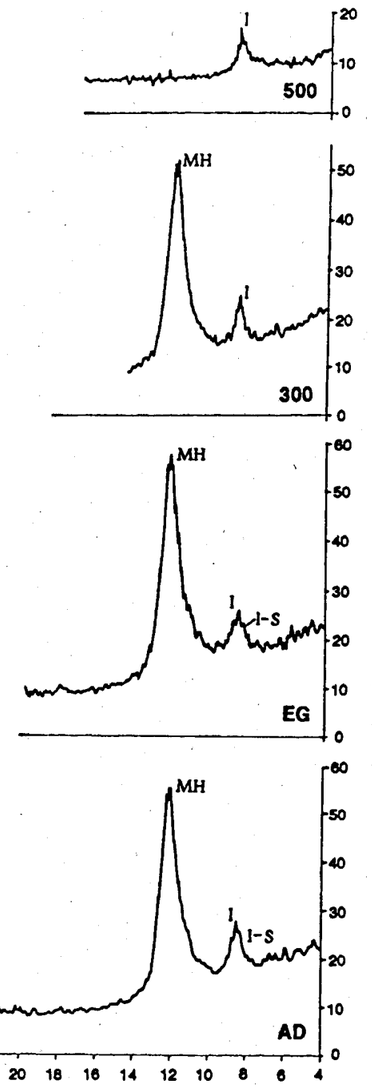
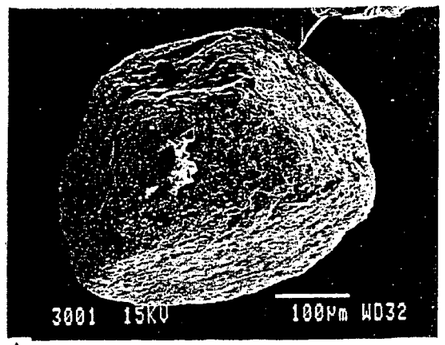
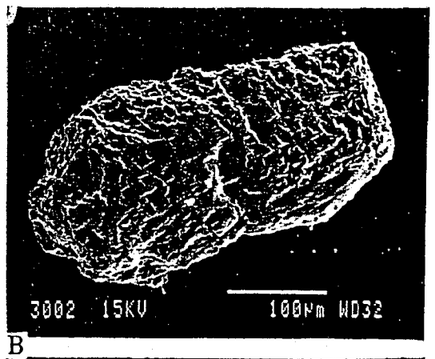


Figure 3. X-ray diffraction pattern of ingested sample 3 from Mahale Mtn. Minerals are identified as: Metahalloysite (MH); Illite-smectite (I-S); Illite (I); Orthoclase (O); Quartz (Q).

Figure 4. A, hematite with a textured surface; B, highly weathered epidote grain; C, etched surface of an epidote grain; D, precipitation of silica on top right of the grain and a clay coating in the centre of the grain; E, two quartz grains on the right and two orthoclase grains on the left; F, minor etching on the surface of an orthoclase grain; G, iron deposits on an intensely weathered quartz grain; H, intensely pitted surface with an iron coat.



A



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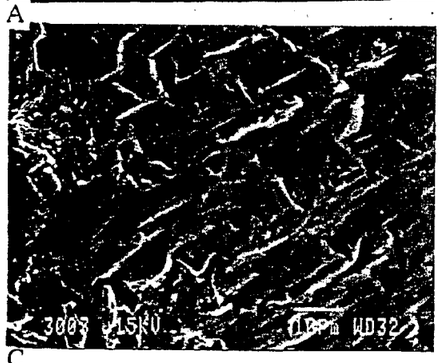

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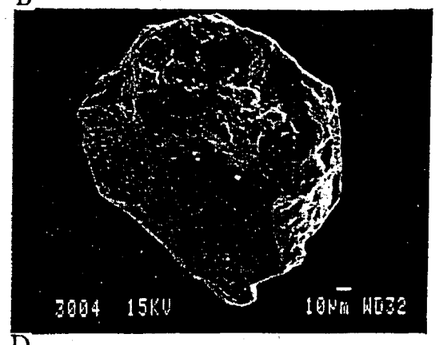

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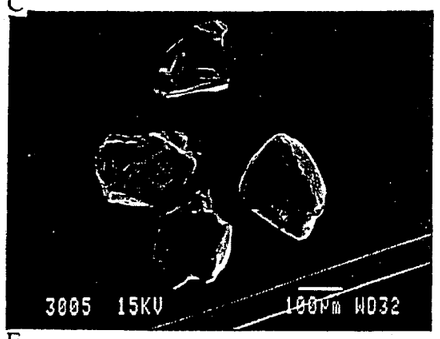

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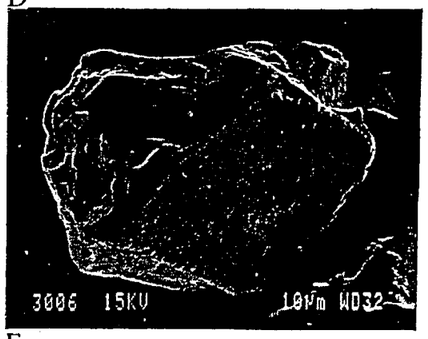

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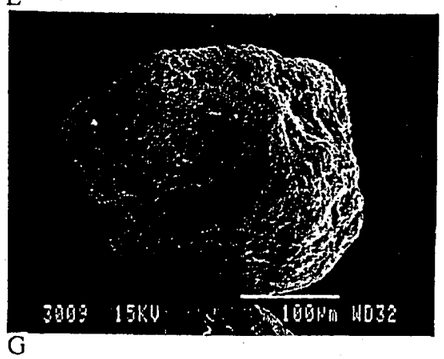

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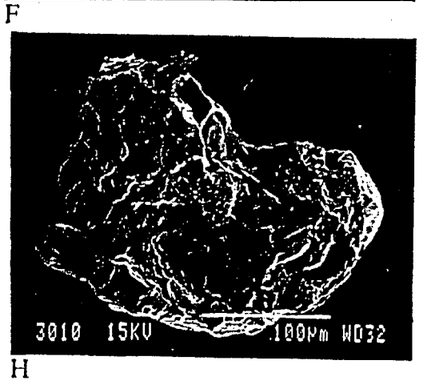

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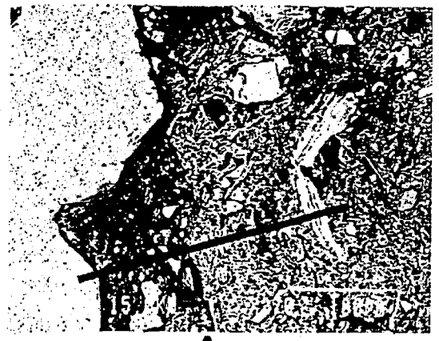
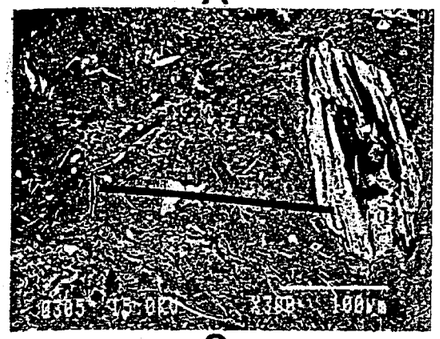


A

B



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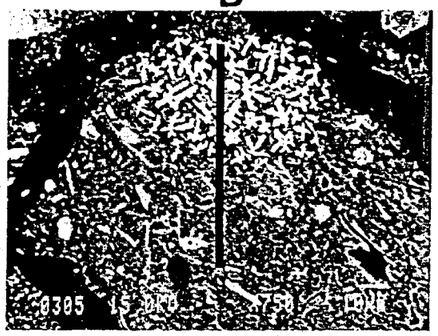

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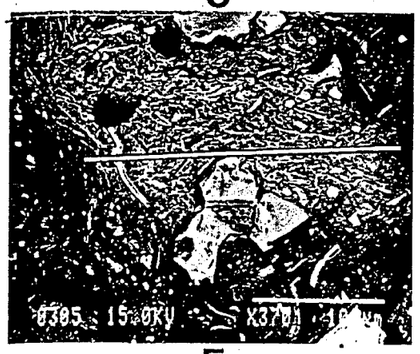

E

Figure 5 Backscatter imagery for control sample 5 and 6 (A), ingested 6 (B), ingested 10 (C, D), ingested 5 (E). A. The line corresponds with the probe transect 3–4 in Table 1. The microprobe transect runs from left quartz grain to the right. Void spaces show up as black areas in the micrograph. Voids in the matrix material could be from sample preparation or from the nature of the matrix. Voids in the mineral grains are *in situ*. B. The line corresponds with the probe transect 5–6 in Table 1. The transect starts at the upper left quartz grain and finishes at an orthoclase mineral in the lower right. The detrital nature of the clay particles can be clearly recognized. C. The line corresponds with the probe transect 7–8 in Table 1. The transect proceeds from right to left starting in a mica grain that is weathering by hydration. D. The line corresponds with the probe transect 9–10 in Table 1. The top end of the transect bifurcates star shaped crystals that are rich in K and Na compared with the adjacent material. E. The line corresponds with the probe transect 11–12 in Table 1. The transect goes from left to right and the large grains under the transect are quartz. The detrital nature of the clay particles are noticeable in the micrograph.

Chemistry

The results of pH, electrical conductivity, the extractable cations (Na^+, K^+, Mg^{2+}, Ca^{2+}), organic carbon and total nitrogen are outlined in Tables 2a and 2b. The pH of every termite mound soil is greater than its matching control sample. In addition, over half of the termite mound samples are moderately basic with pH values between 7.2 and 8.6. The electrical conductivity, which is

Table 2. Chemical properties of sample sets (a) 1 and (b) 2 as pairs of control (c) and termite mound (tm) soils.

(a)

Sample	Set 1	pH (1 : 5)	Soluble salt (S/cm^{-1})	Extractable cations (Cmol kg^{-1}) Ca	Mg	K	Na	$\%C_{org}$	$\%N_{tk}$	C_{org}/N_{tk}
1	tm	8.09	102	4.86	1.19	0.38	0.14	1.3	0.12	10.83
	c	6.15	73	3.36	1.02	0.81	0.04	4.18	0.31	13.48
2	tm	7.16	166	2.71	0.70	0.37	0.04	0.89	0.12	7.42
	c	6.07	80.7	2.94	0.53	0.73	0.03	3.55	0.23	15.43
3	tm	7.67	101	2.99	0.45	0.22	0.05	1.04	0.11	9.45
	c	5.71	84.5	2.97	1.25	0.59	0.04	4.04	0.33	12.24
4	tm	6.10	60.0	1.34	0.98	0.22	0.04	1.14	0.11	10.36
	c	5.55	54.2	2.31	0.98	0.54	0.03	3.46	0.29	11.93
5	tm	8.11	91.5	2.91	1.07	0.36	0.03	0.82	0.11	7.45
	c	5.45	105	2.18	1.55	0.68	0.03	4.16	0.37	11.24
6	tm	6.90	37.1	1.79	1.15	0.55	0.00	0.67	0.10	6.70
	c	5.45	105	2.18	1.55	0.68	0.03	4.16	0.37	11.24
7	tm	7.21	95.5	3.17	0.78	0.28	0.01	0.92	0.11	8.36
	c	5.13	258	2.96	1.27	2.2	0.01	3.46	0.45	7.69
8	tm	8.57	89.1	3.81	0.70	0.19	0.06	0.68	0.08	8.50
	c	5.65	192	2.84	1.68	1.14	0.04	0.94	0.36	2.61
9	tm	8.37	115	4.39	1.15	0.25	0.03	0.68	0.04	17.00
	c	5.44	53.6	2.01	0.49	0.59	0.01	2.13	0.19	11.21
10	tm	6.88	85	2.21	1.03	0.54	0.01	1.48	0.13	11.38
	c	5.02	78.1	2.06	1.02	0.63	0.04	3.65	0.35	10.43

(b)

Sample	Set 1	pH (1 : 5)	Soluble salt (S/cm^{-1})	Extractable cations Ca	Mg	K	Na	$\%C_{org}$	$\%N_{tk}$	C_{org}/N_{tk}
1	tm	7	36.3	5.01	0.86	0.42	0.02	1.09	0.10	10.9
	c	5.49	26.68	1.99	0.9	0.94	0.004	1.26	0.15	8.4
2	tm	6.97	16.96	1.94	57	0.43	0.00	1.12	0.08	14.0
	c	6.56	59.54	3.78	2.09	1.19	0.00	4.23	0.33	12.82
7a	tm	7.48	21.05	3.48	0.9	0.3	0.009	1.50	0.12	12.5
	c	5.41	56.21	3.66	1.56	0.44	0.007	3.66	0.33	11.09
7b	tm	6.58	20.48	3.01	0.9	0.31	0.03	1.04	0.10	10.4
	c	5.3	20.2	1.46	0.61	0.42	0.01	3.12	0.11	28.36
8	tm	7.82	65.64	4.64	1.44	0.59	0.03	1.02	0.09	11.33
	c	6	59.73	3.61	1.19	0.77	0.01	4.17	0.37	11.27
9	tm	7.98	23.53	5.01	0.98	0.25	0.02	0.72	0.07	10.29
	c	5.28	43.63	3.21	1.6	1.05	0.02	4.90	0.40	12.25
10	tm	6.02	42.8	2.39	1.23	0.66	0.01	1.32	0.12	11.00
	c	5.01	13.05	1.61	0.98	0.86	0.01	2.22	0.23	9.65

an estimate of the soluble salt concentration (NO_3^-, Cl^-, SO_4^{2-}), does not reveal any distinct patterns in the data.

The values for Na^+ are extremely low and chlorine is nil. The Ca^{2+} values are quite high and therefore may be available for absorption by the chimpanzee gastrointestinal tract.

The control samples all have a significantly greater amount of organic carbon than the termite mound samples. The termite mound samples have an organic carbon concentration ranging between 0.68 and 1.3% while the control samples range between 1.3 to 4.9%.

An attempt to use t-tests on this data set proved partially conclusive. The pH values are on a log scale and are not subject to analysis by t-test; the ordinal scale numbers for the remainder of the data have a high variability around the mean for each variable; thus, there is low probability that the treatment and control groups come from different populations. However, the t-test results for the ingested samples (estimated P value <0.05) in the tm group show that K, Na and organic carbon are statistically significantly different from the controls. In the recollected set, K, Na, organic carbon and nitrogen are also statistically different from the controls ($P < 0.05$).

Toxin adsorption for sample set 1

Toxin adsorption measurements were carried out to determine the binding properties of the soils to certain alkaloids. Table 3 shows the binding capacities of the soils from data set 1 for four alkaloids. Both control and ingested samples have similar binding capacities and do not differ significantly (χ^2 test, $P > 0.1$).

Table 3. Toxin adsorption analysis of sample set 1, of control (c) and termite mound (tm) soils.

Sample		Adsorption (%) Lupanine	Quinine	Sparteine	Atropine
1	tm	94	98	95	92
	c	94	93	92	–
2	tm	83	88	94	87
	c	91	84	91	87
3	tm	90	96	96	75
	c	85	94	88	27
4	tm	81	82	94	78
	c	80	87	86	85
5	tm	80	93	96	68
	c	84	79	90	72
6	tm	87	92	93	68
	c	84	79	90	72
7	tm	83	91	98	68
	c	81	94	93	–
8	tm	90	94	98	62
	c	87	92	96	50
9	tm	74	94	94	62
	c	76	93	95	88
10	tm	54	89	94	–
	c	58	84	91	78

A slight difference can be seen between the four individual alkaloids which have differing physiochemical properties: mean binding was 73.8 ± 10.1 (SD)% for atropine, 81.6 ± 11.3% for lupanine, 91.7 ± 45.4% for sparteine, and 95. ± 1.75 for quinine; all means except those between atropine and lupanine differ significantly (t-test, $P < 0.05$). An equivalent amount of charcoal would bind 100% of the alkaloids (Wink *et al.* 1993).

Geochemistry

Geochemical analyses, performed on 10 termite mounds and nine control soil samples, allowed determination of the concentrations of major, minor and trace elements. The mean concentrations for 36 elements are displayed in Table 4, along with standard deviations and the mean elemental concentration ratios of ingested to control soils.

Both sets of samples, especially the termite mound group, are relatively high in Al and relatively low in many of the other elements, supporting the finding (above) of a metahalloysite/halloysite mineralogy, with the ingested soils tending to be more Al-rich than the controls. The lower levels of Hf in the ingested samples, relative to the controls, may indicate that the controls are more silica-rich, if Hf proves to be correlatable with zircon.

The ratios of termite mound to control soils also illustrate the differences in elemental concentrations between the two groups of sample material. Approximately 73% of the measurable elements (22/30 elements) have termite mound to control ratios greater than 1, reinforcing the possibility that chimpanzees may be selecting a more enriched material to supplement their diet. While we do not yet fully understand the importance of all of the chemical elements reported here, in terms of nutrition, diet and zoopharmacognosy, the fact that the soils of which they are part are comestible may mean that some, or many, of them have some physiological significance.

Microbiology

The number of microorganisms obtained by dilution plating sample set two (Table 5) varied greatly from sample to sample. Overall, the following patterns were seen in the recollected samples:
(1) unicellular bacteria were more abundant in the control samples than in the termite mound samples in all but samples 2a and 7a; (2) filamentous bacteria were more abundant in the termite mound samples than in control samples except for sample 7a where numbers were equal; and (3) fungi were more abundant in the control samples, except in sample 10.

The control soils contained greater numbers of unicellular bacteria and fungi than termite mound soils. Although the variances were high, there was some indication that unicellular bacteria numbers were not closely correlated with soil type but that filamentous bacteria and fungi could have been.

Table 4. Geochemistry of sample set 1 of control (c) and termite mound (tm) soils. Concentrations in ppm unless otherwise indicated. ⩽: Detection limit at a 68% level of confidence.

Element	tm samples		c samples		tm : c	
	Mean (n = 10)	SD	Mean (n = 9)	SD	Mean	SD
Aluminium (%)	11.2	1.1	8.4	0.5	1.3	0.3
Calcium (%)	0.9	0.8	1.0	0.9	0.9	3.1
Iron (%)	2.8	1.2	2.3	0.5	1.2	1.2
Potassium (%)	2.1	0.5	2.1	0.5	1.0	1.6
Magnesium (%)	0.99	0.21	0.82	0.17	1.2	0.6
Sodium (%)	0.59	0.66	0.68	0.65	0.9	3.5
Arsenic	⩽0.9	0.4	⩽0.88	0.4	⩽1.1	1.5
Barium	1150	150	1190	200	1.0	0.3
Bromine	⩽3.4	0.8	⩽3.0	0.8	⩽1.1	0.7
Cerium	115	24	74	13	1.6	0.7
Chlorine	⩽93	42	⩽100	64	⩽0.9	1.6
Cobalt	8.8	2.4	6.2	1.6	1.4	1.0
Chromium	⩽16.0	2.4	⩽12.0	2.0	⩽1.3	0.5
Cesium	2.0	0.5	1.4	0.3	1.4	0.8
Dysprosium	5.0	1.4	3.0	0.9	1.7	1.2
Europium	2.2	0.4	1.3	0.4	1.7	0.9
Iodine	9.5	5.5	⩽8.0	3.6	⩽1.2	1.9
Gallium	31	14	⩽29.6	22	⩽1.1	2.2
Hafnium	⩽8.8	1.1	⩽10.7	2.3	⩽0.8	0.3
Lanthanum	⩽67	13	⩽39	5.1	⩽1.7	0.7
Lutetium	0.50	0.13	0.29	0.07	1.7	0.9
Manganese	624	203	528	232	1.2	1.2
Neodymium	34	8	18.0	3.5	1.8	1.0
Nickel	⩽22.0	3	⩽18.3	2.2	⩽1.2	0.4
Rubidium	116	23	100	19	1.2	0.5
Antimony	⩽0.14	0.04	⩽0.10	0.02	⩽1.4	0.9
Scandium	13.2	2.7	10.8	3.6	1.2	0.8
Samarium	⩽8.1	1.6	⩽4.8	0.9	⩽1.7	0.8
Strontium	200	90	200	90	1.0	1.3
Tantalum	0.89	0.22	0.86	0.23	1.0	0.7
Terbium	1.1	0.2	0.6	0.1	1.8	0.8
Thorium	17.5	3.9	11.6	1.9	1.5	0.8
Titanium	4750	650	3200	890	1.5	0.6
Uranium	2.9	0.5	2.1	0.3	1.4	0.6
Vanadium	89	21	64	16	1.4	0.8
Ytterbium	3.8	0.7	2.2	0.4	1.7	0.8

DISCUSSION

Both humans (Hunter 1993, Vermeer & Ferrell, 1985) and other animals (Mahaney *et al.* 1996a, Ruggiero & Fay 1994) have been observed ingesting soil from termite mounds. In these studies, the investigators reported that termite mound soil specifically, not the surrounding topsoil, was always selected. In a previous study from the Mahale Mountains by Mahaney *et al.* (1996b) parasitological and behavioural evidence suggested a possible use for the ingestion of termite mound soil for obtaining temporary relief from gastric irritation and/or diarrhoea in chimpanzees. A similar study of geophagy, ingesting exposed clayey substrates, in rhesus monkeys also suggested the antidiarrhoeal properties of the behaviour (Knezevich 1995, Mahaney *et al.* 1995a). In this group of highly parasitized monkeys, geophagy was a frequent occurrence among a large

Table 5. Mean colony forming units (CFUs) $\times 10^{-3}$ g^{-1} of soil of unicellular (UB) and filamentous bacteria (FB) and filamentous fungi (FF) for the re-collected soils of sample set 2.

Sample		c	tm	c : tm
1	UB	21600	23200	0.93
	FB	70	120	0.58
	FF	170	65	2.62
2	UB	72400	6500	11.14
	FB	0	140	0
	FF	2400	13	184.62
7a	UB	5800	2400	2.42
	FB	70	70	1
	FF	10	1.80	5.56
7b	UB	1880	3100	0.61
	FB	0	90	0
	FF	46	3.30	13.94
8	UB	15000	38800	0.39
	FB	50	1000	0.05
	FF	2400	190	12.63
9	UB	21600	72000	0.30
	FB	0	1600	0
	FF	920	80	11.50
10	UB	2400	4000	0.60
	FB	40	150	0.27
	FF	5.20	15	0.35

proportion of its members. Observations of chimpanzees at other sites across Africa show too that at times all members of a group may engage in geophagy on a daily basis (e.g. Goodall 1986). Trends appear to vary from group to group and may be related to seasonal or regional differences in diet as well.

This suggests to us the possibility that geophagy can be a part of their normal foraging routine and supports the fact that mild gastro-intestinal upsets, due to a secondary-plant-rich diet, may also benefit from the properties of ingested termite mound soil. We maintain that regardless of the cause, geophagy has a physiological basis. It is not coincidental that chimpanzees select termite mound soil for consumption even when there is no termite population resident in the mound. The chimpanzees of the Mahale Mountain group have not been observed to habitually feed on termites in the 35-plus y of research. They fish for carpenter ants in trees but not termites in mounds. Furthermore, at sites where termite mounds are not present or obvious, animals select the clayey soils, brought up to the surface by fallen trees or from areas of exposed hillside. Subsurface soil brought to the surface and used to build the mound is the subject of this investigation. Therefore an understanding of the physical and chemical properties of termite mound soil is relevant.

The higher Hf concentrations reported for the control soils may correlate with higher amounts of zircon in them, a relationship resulting from a selective avoidance of heavy minerals by the termites in mound construction. This relationship should be explored in depth with a larger population of samples.

The concentrations of the majority of chemical elements detected in our analyses were greater in the termite mound samples than in the control group.

The effect of termite mound-building in East Africa on soil properties have been studied extensively in the past (Arshad 1981, Hesse 1955, Lee & Wood 1971, Pomeroy 1976). One of the predominant features of termite activity is their influence on the structure of their ecosystem. For example, termites will chemically and physically alter the soil from its original composition when constructing their mounds. This alteration may form a soil with a clay and mineral-rich composition often derived from considerable depth beneath the surface, possibly producing a soil matrix more desirable for ingestion.

Results from experiments performed on termite mound soil from East Africa have shown increased concentrations of major elements such as calcium (Arshad 1981, Hesse 1955, Watson 1975), magnesium (Lee & Wood 1971, Woods & Sands 1978) and potassium (Lee & Wood 1971, Woods & Sands 1978). Ore-forming elements, such as chromium (Prasad & Saradhi 1984), vanadium (Prasad & Saradhi 1984) and uranium (Le Roux & Hambleton-Jones 1991) have also been found to be more concentrated in termite mound soil. With respect to the medical implications of geochemically enriched soil, it can act as protection against diseases caused by nutritional deficiencies. The consistent difference between the termite mounds and nearby control soils suggests that the chimpanzees may be critically selecting a chemically enriched clayey natural earth to supplement their diet. The well-weathered minerals in the termite mound soil undoubtedly provide a great range of chemical elements to the foraging chimpanzees. As shown by SEM analysis, the prevalence of altered hematite and epidote provide Fe and Ca. Indeed, the prevalence of Fe coatings on orthoclase and quartz sands, which prevail in the termite soils reported here, strongly support the interpretations of a previous study in the same area (Mahaney *et al.* 1996b). This relationship is also supported by the electron microprobe data that show higher Fe in the termite mound samples relative to the control group.

Mahaney *et al.* (1996b) suggested that K and Fe, if in a form available for absorption by the gastro-intestinal tract, could have nutritional importance. Iron levels found here in the termite mound soil average 3.3%, which is high enough to provide a chemical benefit when ingested. The high levels of Fe, as indicated from the soil colours, and verified by INAA in both groups of soil, may be important to chimpanzee health. However, the control group soils are suspected to contain undesirable properties (e.g. bacterial contamination) as indicated by darker colours, and higher organic carbon content.

In this study total K is most likely not a highly important benefit of geophagy. Data set 1 has a ratio of <1 and data set 2 (not reported here) has a termite mound over control ratio equal to 1. Exchangeable K, however, as reported in Tables 2a and 2b shows that termite mound soil is statistically different from the control group. Overall, the greater concentrations of all chemical elements seen in the termite mound soils, compared to the topsoils, suggest that chimpanzees can obtain adequate amounts of them by ingesting

termite mound soil. Moreover, the higher pH of these soils, commonly observed in tropical soils (Sanchez 1976), may increase nutrient availability. The higher pH also indicates that termite mound soils could have an antacid action in the gut.

The soil chemistry shows little statistical difference of total salts, exchangeable Ca and Mg, and C/N ratios between the termite mound and control soils, which eliminates them as possible stimuli in this case.

The most important characteristic of soils used for mound construction is the proportion of sand, silt and clay (Lee & Wood 1971). Studies have shown that the mounds are generally richer in clay than the surrounding soil (Hesse 1955, Lee & Wood 1971). This may be because the mounds are built from subsoil that is richer in clay than the surrounding topsoil (Hesse 1955). Termite mounds are generally not found on sands where there is inadequate binding material, i.e. clay (Goudie 1988).

In this study, particle size analysis shows that all termite mound samples contain *c.* 20% more clay than the surrounding soil. Finer grained soils offer a greater surface area for acid extraction of nutrients at gastric pHs and increase the uptake of toxins by clay mineral surfaces. Finer grained material also offer a safer alternative to forest floor soil as they are likely to contain lower levels of harmful soil-inhabiting-stage parasite larvae and ova. Moreover, the hardness of the mound material is no doubt related to alternating wet and dry climatic cycles throughout the year with the dry part of the cycle creating an armouring effect that preserves the mound once constructed.

In most studies of geophagy in animals, the soils contain clay minerals which are 1 : 1 layer silicates (Mahaney *et al.* 1995a,b, 1996a, 1997). Humans also prefer to ingest 1 : 1 clay minerals and the reason suggested for this has been that 2 : 1 minerals may absorb required nutrients, such as Fe and Zn, unlike the 1 : 1 clays that are not as effective (Vermeer & Ferrell 1985).

The 1 : 1 clay minerals play an important role as a base for pharmaceutical preparations aimed at remedying gastro-intestinal problems. Specifically, kaolinite forms a protective cover on the mucous membrane of the digestive tract and adsorbs bacteria and toxins (Vermeer & Ferrell 1985). Kaolinite is considered quite safe for internal use, as it is a chemically pure mineral (Vermeer & Ferrell 1985). Metahalloysite, the 1 : 1 clay mineral found in most of the ingested samples, may adsorb tannins and toxins that the chimpanzees would otherwise not be able to detoxify (Hladik 1977, Oates 1978). Since chimpanzees eat large amounts of leaf material, along with fruits in various stages of ripeness, they cannot avoid contact with dietary toxins or antinutrients that most plants produce in defence of herbivores and other plant predators (Wink 1993b). In general, the controls and termite mound soils were found to effectively bind alkaloids considered to be typical animal toxins in plants (Wink 1993b). In many leaves, alkaloid concentrations range from 100 to 500 $\mu g\ g^{-1}$ fresh weight. According to Table 3, 100 mg of soil would be adequate to bind most of the alkaloids present in 1–10 g of leaves.

The chimpanzees of the Mahale Mountains have been closely observed since 1965 (Nishida *et al.* 1983, Nishida 1990). As part of this work, the plant food available to the chimpanzees has been well documented (Nishida & Uehara 1983). Chimpanzees forage on the leaves, bark and pith of a variety of different plant species and the levels of condensed tannins in many of these wild tropical plants are quite high (Gartlan *et al.* 1980). Condensed tannins, which are plant secondary metabolites, may have detrimental effects in many mammals by reducing protein digestibility (Mole & Waterman 1987). Since the concentrations of these chemicals are sometimes high enough to be toxic, animals without specialized guts may adopt methods of detoxification in order to tolerate the tannin levels in their diet. In veterinary medicine, it is common practice to use kaolin as an antacid (Daykin 1960). The clays in termite mound soil could also function as an antacid in response to dietary imbalances. Over half of the samples had pH values between 7.2 and 8.6. The termite mound soils might act as a buffering agent to counteract the effects of acidic foods. It is assumed that chimpanzees would benefit from the antacid effects of termite mound soil the same way humans obtain relief from the pharmaceutical Kaopectate™.

Detoxification is a likely benefit of geophagy, as all termite mound soils displayed superior alkaloid-binding capacities. It was shown that the alkaloid adsorption capacities of both the termite mound and control samples were comparable. However, micro-organisms found in forest floor soils (control samples) are directly related to the organic matter content so that areas rich in organic matter have the largest bacterial numbers. Some microbes found on the forest floor can cause disease or in extreme cases death if ingested.

It is particularly interesting that fungi are usually higher in control soils while filamentous bacteria are higher in the ingested termite mound soils. With respect to geophagy, it would appear that chimpanzees are selecting soils relatively high in filamentous bacteria, except for sample 7a. However, it may not be a matter of this sample being low in filamentous bacteria, but of the control sample being somewhat high. Similarly, the other example where fungi are higher in the ingested sample (sample 10), is because fungi are low in the control sample, not high in the termite mound sample.

The filamentous bacteria are probably all members of the genus *Streptomyces*, which are the most prolific micro-organisms known in the production of medically useful secondary products such as antibiotics. Fungi, while producing some antibiotics, such as penicillin, are also notorious for producing extremely toxic metabolites (Miller 1995). By consuming the soil of termite mounds, instead of top soil, chimpanzees may be avoiding toxic fungi, or obtaining higher than normal doses of *Streptomyces* products. As these speculations are highly premature intensive microbiological investigations of soils consumed by chimpanzees are presently being conducted.

In conclusion, geophagy in chimps appears to be a multifunctional behaviour

ranging from dietary (e.g. mineral supplementation) and medical benefits (antacid and antidiarrhoeal properties) to the detoxification of dietary secondary metabolites (such as alkaloids). Because of these many-sided benefits, it is not surprising that geophagy has a wide distribution in animals and humans.

ACKNOWLEDGEMENTS

Field work and sample collection by MAH in Tanzania was supported in part by grants and funds from Plant Sciences Research Foundation of the Faculty of Agriculture, Kyoto University and the Wellcome Trust, UK. Special thanks goes to T. Kishida and K. Ueno of the Pasteur Institute of Medical Research, Kyoto, for technical support and to N. Ito, Mohamedi S. Kalunde, K. Kawanaka, M. Nakamura and T. Nishida for their assistance and friendship in the field. We wish to give our sincerest gratitude to the administration and staff of the Tanzanian National Scientific Research Council, Tanzanian National Parks, Tanzanian Wildlife Research Institute and the Mahale Mountains Wildlife Research Centre. We also thank the Natural Sciences and Engineering Research Council of Canada for an Infrastructure Grant to the SLOWPOKE Reactor Facility of the University of Toronto. The mineralogy and soil chemistry components of this research were supported by grants to WCM from the Atkinson College Minor Research Grant Fund.

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Ethology **106,** 105—116 (2000)

ISSN 0179–1613

RESEARCH PAPERS

Instituto Piernaico de Ecologia (CSIC), Zaragoza, and Primate Research Institute, Kyoto

Fractal Long-Range Correlations in Behavioural Sequences of Wild Chimpanzees: a Non-Invasive Analytical Tool for the Evaluation of Health

C. L. Alados & M. A. Huffman

Alados, C. L. & Huffman, M. A. 2000: Fractal long-range correlations in behavioural sequences of wild chimpanzees: a non-invasive analytical tool for the evaluation of health. Ethology **106,** 105—116.

Abstract

Quantitative evaluation of health impairments in wild chimpanzees was explored using fractal long-range correlations of behavioural sequences. The health status of 13 chimpanzees in the Mahale Mountains National Park, Tanzania was evaluated non-invasively using standard behavioural observation and parasitological analysis of stool samples. Based on these data, individuals were classified as being either healthy or sick. Behavioural sequences were analysed and shown to exhibit long-range power law correlations. The behavioural sequences of individuals in healthy and sick states were quantitatively evaluated using detrended fluctuation analysis of social and non-social behaviours within behavioural sequences. These values were compared and significant differences in long-range correlations were found between health states. Sex differences were also noted, with female social behaviour displaying a larger fractal dimension than male social behaviour. The fractal dimension of females declined significantly in sick individuals. This analysis of behaviour provides a new and effective non-invasive method to record and evaluate the general state of health and related stress of animals in the wild. Possible applications of this method in captive situations include the monitoring and evaluating of stress levels over time.

Corresponding author: C. L. Alados, Instituto Piernaico de Ecologia (CSIC), Avda. Montanana, 177, Apto 202, 50080 Zaragoza, Spain. E-mail: alados@ipe.csic.es

Introduction

Fractal analysis of behavioural sequences has proved to be an effective tool for the non-invasive assessment of the general health of wild animals (Alados et

al. 1996). Fractal structures are considered to have 'scale symmetry', that is, they look the same on many different scales of magnification. Fractal objects in nature are considered to be either random or statistically self-similar. They are differentiated from non-random fractals, which look exactly the same at infinite length scales (Mandelbrot 1982; Bunde & Havlin 1994). A fractal process occurs when the distribution of an event on a temporal scale presents a fractal structure. These processes have statistical self-similarity on all scales. The fractal structure of time series has traditionally been investigated by 1/f noise (Voss 1988; Schroeder 1991). The significance of analysing time series such as behavioural sequences lies in whether the observed variations are due to random phenomena or in fact arise from deterministic interactions of several variables whose number and type are generally unknown. The duration of behavioural sequences displays complex patterns that reveal apparent non-random periodicities in the case of interscan intervals (Quenette & Desportes 1992). Cole (1995) and Escos et al. (1995) observed that behavioural sequences have a self-similar structure that may provide a powerful tool for understanding the temporal structure of behaviour.

Behavioural sequences, though they often appear erratic, reveal 1/f like spectra (Alados et al. 1996), but long-term correlation properties of behavioural sequences have not been directly investigated except in fathead minnows (*Pimephales promelas*) (Alados & Weber 1999). Long-range correlations have been observed in heart-beat intervals, DNA nucleotide sequences (Stanley et al. 1992) and in the stride interval of the human gait (Hausdorff et al. 1995). This indicates that these time series are neither random (white noise) nor the result of only short-term correlations, but rather the result of highly organized complex processes that may generate long-term autocorrelation.

In recent years an increasing number of studies are demonstrating the importance of fractal analyses to discriminate morphological structures and time series that may be used in diagnosis, and that may be quantitatively characterized by the fractal dimension (Bassingthwaighte et al. 1994). For example, the fractal dimension of an electroencephalogram declines with the advancement of Alzheimers disease (Woyshiville & Calabresa 1994). Heart rate variability spectral analysis has been used to detect cardiovascular complexity alterations, indicating that reduced complexity might be incompatible with cardiovascular homeostasis (Butler et al. 1993). Stride interval fluctuations also present a fractal scaling property that depends on body condition. Elderly subjects and subjects with Huntington's disease present more random fluctuations than young, healthy individuals (Hausdorff et al. 1997).

As part of a long-term study in progress investigating behavioural adaptations for the control of parasite infection and other forms of self-medication in African great apes (Huffman 1997), longitudinal parasitological and behavioural data have been collected from known individuals of the fully habituated Mahale M group of wild chimpanzees (*Pan troglodytes schweinfurthii*) in western Tanzania (e.g. Huffman et al. 1993, 1996, 1997). Short-term changes in health status vary from the dramatic (Huffman & Seifu 1989; Huffman et al. 1993) to the often more subtle (Huffman et al. 1996). Available measures of health status, such as parasite load,

when considered alone, can be problematic as the effects may vary from individual to individual. The same parasite load may have a greater impact on some individuals than on others, depending upon the overall stamina and fitness of the individual (e.g. Huffman et al. 1997). An independent and supplementary measure of physical condition which allowed statistical comparison would enable better assessment of health status and changes thereof over time. In this paper we investigate whether fractal analysis of long-range correlations of behavioural sequences can be used to assess the health condition of wild chimpanzees.

Methods

Chimpanzees of the Mahale M group were observed by focal animal sampling, recording, as precisely as possible, the onset and ending of all behavioural sequences and events (Martin & Bateson 1993). The behavioural data used in the following analyses were collected by M.A.H. from 13 individuals (six females and seven males) between Nov. 2 and Dec. 28, 1991. Table 1 shows the major categories into which observed behaviours were classified.

For this study, we selected behavioural sequences from the focal data in which the animals spent more time in active social behaviours. To do this, we removed observations where the focal animal was resting at the beginning or the end of the sequence to avoid sequence interruption, given that it is the correlation between times of the sequence that we are interested in. For calculations, each change in activity from active social behaviour (S, SP and SGG) to the other behaviours (SS,

Table 1: Behaviours used in coding behavioural sequences

Active social behaviours	
SP	social play, i.e. wrestling, play chase, etc.
SGG	grooming others, mutual grooming
S	miscellaneous behaviour directed at others, i.e. courtship, agonistic displays, copulation, chase, supplant, self-grooming and approach
Other activities	
SS	sitting in a social gathering without mutual interaction; pause between activities
SR	sitting and resting in a social gathering or alone; rest intervals between other activities; stationary activities, sitting up, looking around, inanimate substrate manipulation, etc.
SGR	unidirectional receipt of grooming
L	lying down in day bed on ground or in tree to sleep
F	feeding-foraging; includes time spent moving from one patch to another, but not stopping between feeding bouts for more than 5 min
T	travelling, moving between places; activities, taking few rests, rarely pausing to sit and rest
M	moving; intermittent rests, moving slowly and pausing to rest for periods frequently as long as time spent walking; not intermixed with other activities

SR, SGR, L, F, T and M) and vice versa was used, including short-term events such as when an animal changed grooming partners. Descriptions of the behaviours used in this evaluation are given in Table 1. Active social behaviour was defined as those behaviours displayed when the subject was involved in social interactions as the actor, and the receiver was its companion. The total amount of time for which the animal was observed in each behavioural sequence was divided into 5-s intervals in order to make the sequence easily computable without loosing accuracy, granted that the duration of an activity was never shorter than 5 s. The total duration of data recording per focal individual is presented in Table 2, while per individual sequence duration in 5-s units is presented in Table 3.

The general state of health of an individual during focal observations was non-invasively evaluated using multiple qualitative and quantitative measures of health adopted from standard preliminary veterinary diagnosis in the field. The measures used were visual classification of stool type (diarrhoeal or normal), presence/absence of adult parasites in the stool, microscopic analysis of intestinal parasite infection and qualitative behavioural signs clearly indicative of health status such as appetite, stamina and such obvious involuntary behaviours (coughing, sneezing, flatulence, wheezing, etc.) indicative of illness and/or a physiological imbalance. Based upon these observations, individuals were then classified as being either sick or healthy on the day on which data were used for the following analyses. Individuals displaying at least three of these independent measures of ill health were classified as sick. No attempts were made to grade health on a point scale. The diagnostic symptoms observed and health status assigned to each case are given in Table 2.

Detrended fluctuation analysis (DFA) was performed to measure the correlation between data sequence points for a one-dimensional random walk. The method is described by Peng et al. (1992), and its posterior modification in Peng et al. (1994). The procedure applied to behavioural data is detailed in Alados & Weber (1999). It has the advantage that it removes local trends and, in consequence, is not affected by non-stationarities. A time series is stationary if there is no systematic change in mean (no trend), and if strict periodic variations have been removed. In many series these conditions are violated.

Applying the method of Peng et al. (1992), we examined a binary sequence [z(i)] of active or social behaviour denoted by 1, and non-active or non-social behaviour denoted by –1 at 5-s time intervals (i) taken from continuous observations. We can generate a behaviour sequence random walk, y(t), obtained by adding the previous sequence such that $y(t) = \sum_{i=1}^{i=N} z(i)$. This provides a graphical representation that permits calculation of the degree of correlation in the behaviour time series. The entire sequence of data of length N is divided into non-overlapping subsequences, or 'boxes', of length b. In each box we fit a least square line to the data. Let $\hat{y}_b(t)$ be the regression estimate of $y_b(t)$ for each box size b. The fluctuation of $y_b(t)$ about $\hat{y}_b(t)$ was calculated for each data point, and then averaged fluctuation for that box size b was determined as

$$F^2(b) = \frac{\sum[y_b(t) - \hat{y}_b(t)]^2}{N}.$$

Table 2: Records of health status used in qualitative evaluation of individuals used in fractal analysis (Huffman et al. 1996, 1997)

Name	Date	Focal (h)	Status	Observational and parasitological evaluation of health status
BO (OAF)	91.11.15	7.43	sick	out of nest later than others; malaise; frequently sleeps; low O.s. infection
GW (AF)	91.11.18 $_1$	2.78	healthy	appetite; o parasite infection detected; interacts socially with others
	91.12.28 $_2$	3.76	sick	malaise; frequently sleeps in day bed; deep cough, constipation, low S.f. infection
FT (AF)	91.11.19 $_1$	4.28	healthy	appetite; normal stools; no parasites detected
	91.12.23 $_2$	3.46	sick	malaise; frequent sleeps on ground; severe diarrhoea, flatulence, med. O.s. infection
WL (AF)	91.12.02	4.25	sick	malaise; frequently sleeps in day bed; lags behind group; med. O.s. infection
TY (AF)	91.11.11 $_1$	6.24	sick	frequent defecation; diarrhoea, runny nose, bronchial congestion, no parasite infection detected; in night bed early
	91.11.12 $_2$	8.10	sick	out of bed later than others; malaise; frequently sleeps, rests; appears to have lower back pains; no parasite infection detected
WA (AF)	91.11.05	6.20	sick	malaise; frequently sleeps; appears weak, lags behind party; deep cough, constipation, low O.s. infection
BA (AM)	91.12.13	4.90	sick	runny diarrhoeal stools; low E.c infection; interacts socially with others
AJ (AM)	91.11.28 $_1$	7.78	sick	malaise; thin; often attempts to defecate in crouched posture; later diarrhoea; expels worms, high O.s. infection; interacts socially with others but moves off to rest alone later
	91.12.16 $_2$	4.58	sick	often attempts to defecate; later diarrhoea; expels worms, med. O.s. infection; moves off from others and rests alone; lower back pain, flatulence
NS (AM)	91.11.30	5.45	healthy	socially active; courtship; aggressive displays
MU (AM)	91.11.09	4.47	healthy	socially active; no parasite infection detected
TB (ADM)	91.11.07	5.39	sick	socially active; courtship observed but builds ground cushions or day nest and often sleeps; low O.s. infection
	91.11.16	5.42	healthy	no parasite infection detected; socially active; good appetite
DE (AM)	91.11.04 $_1$	5.52	healthy	socially active; courtship; good appetite; agonisitic display; low E.c. infection
	91.12.04 $_2$	5.52	healthy	socially active; good appetite
MA (AM)	91.11.02 $_1$	1.20	sick	socially active; courtship; runny nose, flatulence, diarrhoea
	91.12.07 $_2$	7.53	sick	frequently sleeps in day beds; often sits alone; some social interaction; low T.t. infection

OAF: old adult female (over 41 years old); AF: adult female (15–40 years old); AM: adult male (16–40 years old); ADM: adolescent male (8–15 years old); O.s.: *Oesophagostomum staphanostomum*, E.c.: *E. coli*; T.t. : *Trichuris trichiura*.

Table 3: Alpha exponent and curve fitting estimator (R2) of the equation $F(b) \cong b^{\alpha}$ for portion of behavioural sequences used in analysis

Name	Date	Sequence(s)	Status	Alpha	R^2
BO (OAF)	91.11.15	3588	sick	1.120	0.963
GW (AF)	91.11.18 $_1$	2712	healthy	1.140	0.974
	91.12.28 $_2$	2005	sick	1.280	0.994
FT (AF)	91.11.19 $_1$	3084	healthy	0.910	0.951
	91.12.23 $_2$	2496	sick	1.260	0.982
WL (AF)	91.12.02	3062	sick	1.340	0.989
TY (AF)	91.11.11 $_1$	4490	sick	1.202	0.977
	91.11.12 $_2$	3312	sick	1.137	0.947
WA (AF)	91.11.05	3752	sick	1.281	0.994
BA (AM)	91.12.13	2940	sick	1.291	0.994
AJ (AM)	91.11.28 $_1$	5604	sick	1.221	0.987
	91.12.16 $_2$	3300	sick	1.246	0.986
NS (AM)	91.11.30	3925	healthy	1.295	0.994
MU (AM)	91.11.09	3216	healthy	1.412	0.994
TB (ADM)	91.11.07 $_1$	3520	sick	1.248	0.989
	91.11.16 $_2$	2340	healthy	1.281	0.994
DE (AM)	91.11.04 $_1$	3972	healthy	1.260	0.985
	91.12.04 $_2$	3971	healthy	1.280	0.991
MA (AM)	91.11.02 $_1$	2513	sick	1.295	0.992
	91.12.07 $_2$	5045	sick	1.436	0.992

OAF: old adult female (over 41 years old); AF: adult female (15–40 years old); AM: adult male (16–40 years old); ADM: adolescent male (8–15 years old).

If this procedure is repeated for various box sizes, b, the residual variances should fit the relation

$$F(b) \cong b^{\alpha}$$

where $\alpha = 1/2$ indicates no correlations in the sequence (white noise), and $\alpha \neq 1/2$ indicates long-range power law correlations (the social interaction bout length depends on the history of the actors' social patterns). If α exceeds 1/2, the sequence is persistent; if $\alpha < 1/2$ the sequence is anti-persistent (a long bout is more likely to be followed by a short one and vice versa). We considered boxes of size nearest integer to 2^2, $2^{2.5}$, 2^3,...2^9. The box sizes were equally spaced on a log scale to avoid biasing the linear regression in favour of the larger box sizes.

Results

Fig. 1 presents scatter plots of the behaviour sequence for an adult female (GW) when classified as sick and again as healthy on another day. We generated a random walk, y(t), obtained by successive addition on the binary sequence,

Fig. 1: Behavioural sequence walks for an adult female (GW) when classified as sick and healthy. X-axes represent the time in 5-s units. a. Y-axes represent the binary behavioural sequence [z(i)] (1 for active social behaviour and –1 for activity-lag). b. Y-axes represent the generated random walk, y(t), obtained by adding the previous sequence such that $y(t) = \Sigma_{i=1}^{i=N} z(i)$. c. Fluctuation analysis; X-axes represent the natural logarithm of box size (b); Y-axes represent the natural logarithm of the average fluctuation [F(b)]; the α exponent is the slope of the regression equation

providing a graphical representation that permits calculation of the degree of correlation in the behaviour time series. Calculation results of each chimpanzee analysed are presented in Table 3. The average α value for the 13 chimpanzees analysed is $\alpha = 1.247 \pm 0.02$, $n = 20$ behavioural sequences. Our results reveal that the social behaviour sequence exhibits long-range power law correlations, that is the present behaviour depends on long-term activity. DFA analyses of randomized data sets of six different sequences give an average α value of 0.5 ± 0.006, close to the 0.5-value of random fluctuation of infinite length sequences, significantly

different ($t = 9.67$, $df = 4$, $p < 0.001$) from the social behaviour sequence of chimpanzees. That is, randomly shuffled data are not autocorrelated; the direction of each step is independent of previous steps. However, in the autocorrelated behaviour sequences of chimpanzee social activity, the direction of the step depends on the history of the walker. Additionally, high accuracy of curve fitting is observed for the DFA analysis ($R^2 = 0.984 \pm 0.003$, $n = 20$).

In order to gain insight into the underlying conditions for this long-term dependence, we investigated the effects of health status and sex on social behaviour sequence correlations. Because time length sequences are not the same in all observations, one-way analysis of covariance was performed with time length included as a covariant. The results showed no significant effect of sequence duration on the alpha exponent ($F_{1,14} = 0.24$, ns). In consequence the covariate was eliminated in posterior analyses. Female social interval fluctuations increased slowly with time scale ($\alpha = 1.128 \pm 0.034$, $n = 9$), in comparison with males ($\alpha = 1.297 \pm 0.027$, $n = 10$). In general α is equivalent to the Hurst exponent H (Hausdorff et al. 1997), and it is inversely related to the fractal dimension by the relation $H = 2 - D$, for one-dimensional series. In consequence, we can say that female social behaviour presents a larger fractal dimension, that is, it is more complex than male social behaviour. This effect is significant only when healthy individuals are analysed (Table 4). Additionally, healthy chimpanzees present lower α figures (1.165 ± 0.036, $n = 7$) than do sick individuals (1.26 ± 0.025, $n = 12$), but because an interaction between sex and body condition exists ($F_{1,15} = 6.46$, $p < 0.05$), two separated one-way ANOVAs were performed (Table 4). The results showed a change in the slope of the power law relation between the root mean square fluctuation [F(b)] about the average displacement and box size (b) for individuals belonging to different categories. Healthy females have significantly lower α values than do sick females. That is, the fractal dimension, inversely related to the α exponent, declined in sick individuals.

Discussion

The calculation of α using DFA provides a new quantitative method to measure the degree of correlation in behavioural sequences, and to analytically distinguish healthy from sick individuals. In this study we addressed the question

Table 4: Fractal complexity of social behaviour time series. $\bar{x} \pm$ SE (n), α values and F values of the one-way analysis of variance

	Healthy	Sick	F
Males	1.306 ± 0.033 (5)	1.289 ± 0.033 (5)	$F_{1,8} = 0.12$, ns
Females	1.025 ± 0.069 (2)	1.232 ± 0.037 (7)	$F_{1,7} = 7.02$, $p < 0.05$
	$F_{1,5} = 13.64$, $p < 0.05$	$F_{1,10} = 1.39$, ns	

of whether behaviour sequence fluctuations are due to long-range correlations, where present behaviour depends on past history of activity ($\alpha > 0.5$), or whether they are simply random fluctuations or the consequences of short-range correlations ($\alpha = 0.5$). We observed that social behaviour sequences are long-term correlated, that is the present behaviour depends on long-term activity, and thus, the fractal properties of the behavioural sequence are characterized by a power law scaling of the correlation, as observed in numerous phenomena having a fractal origin. For example, 1/f temporal fluctuations are found in the heart rate of healthy individuals (Kobayashi & Musha 1982; West 1990; Meesmann et al. 1993), respiratory intervals in animals (Kawahara et al. 1989) and neuronal discharges during sleep (Yamamoto et al. 1986). The mechanisms responsible for the long-term correlations in the behavioural sequences are still unknown, and their function remains to be determined. Several authors have suggested long-term fluctuations as mechanisms to maintain stable homeostasis in living systems (Butler et al. 1993; Uritsky & Muzalevskaya 1993). These fluctuations may be influenced by the environment to the point that it has been reported that low electromagnetic 1/f fluctuations have a stabilizing effect on many biological processes and can act as a powerful therapeutic agent (Uritsky & Muzalevskaya 1993).

In general, we observed that, among chimpanzees classified as being healthy on behavioural and parasitological measures, males presented more predictable behavioural sequences than females. Also, healthy females presented higher fractal dimensions than sick females. This change is similar to that observed in power spectrum analyses of female Spanish ibex (*Capra pyrenaica*) (Alados et al. 1996). The different scaling of behaviour sequences of healthy and sick individuals must be related to the underlying dynamics of physiological components. In consequence, fractal-like fluctuations in the behaviour sequence may be a feature of the behaviour system that reveals the health condition of individuals. Thus the change in the fractal dimension of behavioural sequences may be an indicator of influences of the state of health on temporal patterns.

Changes in the fractal structure of behavioural sequences have also been reported in toxicological studies, revealing a reduction in the fractal dimension of locomotor activity in rats under the effects of toxic substances (Motohashi et al. 1993), or the complexity of reproductive fish behaviour under Pb exposure (Alados & Weber 1999). According to Buldyrev et al. (1994), long-range correlation in biological systems is adaptive because it serves as an organizing principle for highly complex, non-linear processes, and because it prevents restriction of the functional response of an organism to a highly periodic behaviour. When physiological systems (Goldberger 1997) and behavioural responses (Alados et al. 1996) lose their fractal complexity, they reduce the efficient transport of substances and information over a complex interacting system. As a result, they are less adaptable and less able to cope with the exigencies of an unpredictable changing environment (Goldberger 1997). Comparisons of interbeat intervals of healthy subjects and patients with severe cardiac disease showed that healthy heartbeat time series present more complex fluctuations than diseased heart fluctuations. However, not all the studies have reported a fractal dimension increase with health status. Hausdorff et al.

(1997) observed that complexity of stride intervals in humans increases with age and Huntington's disease. These contradictory results must be related to the advantages of performing one or another behaviour. A steady path probably confers a greater advantage to prevent overbalancing. On the other hand, scanning unpredictability is considered to be an adaptive strategy (Pulliam 1973; Lendrem et al. 1986) because the probability of detecting a predator depends, in part, on the pattern distribution of scanning sequences. Similarly, the structural patterns of social activity intervals may have important implications for anti-predator behaviour given that, when chimpanzees are occupied interacting with each other, they lose predator awareness.

The fact that male chimpanzees, unlike females, do not change the complexity of their social activity when they are sick may be interpreted as reflecting the different underlying mechanisms leading to social behaviour in each sex. Similarly, a study (Alados & Webber 1999) on fish behaviour under Pb exposure revealed that the complexity of the reproductive behaviour of males fishes after sexual maturity did not change significantly, while the fractal complexity declined under 0.5 p.p.m. Pb exposure before sexual maturity.

Further investigations are needed to elucidate long-range correlation of behavioural sequences. Some questions remain to be answered. Which behavioural sequences are more tolerant of internal and environmental perturbations? How stable is the degree of correlation in the behavioural time series under identical conditions? What is the range of variation in the scaling exponent of those sequences? Because the accuracy of analysis is limited by the length of the available behavioural sequences, it is important to investigate the effect of finite length on the exponents calculated and to estimate the optimal length sequence needed for a high-accuracy estimation of health status. Some will argue that health status is a point on a continuum. It is not the purpose of this paper to grade states of illness but to evaluate observable differences in health status using detrended fractal analysis as an independent analytical tool.

From this study we conclude that behavioural sequences are heterogeneous over time in a non-random pattern, showing long-range correlation. We also conclude that DFA analysis is a dynamic, non-invasive technique to quantify changes in body conditions and may be a useful method for evaluating the behavioural effects of environmental variables. From a wildlife conservation standpoint, this may prove to be an indispensable method for monitoring and assessing the long-term impact of such factors as eco-tourism or habitat degradation on endangered species like the chimpanzee. In captive situations, DFA analysis may prove useful in monitoring or evaluating the effects of environmental enrichment programmes on the stress levels of animals. From a wildlife conservation standpoint, this may prove to be an indispensable method for monitoring and assessing the long-term impact of such factors on chimpanzee in their natural habitat.

Acknowledgements

We thank the people and Government of Tanzania for their long-term cooperation and commitment, in particular the Tanzanian National Scientific Research Council, Tanzanian National Parks, Serengeti Wildlife Research Institute, Mahale Mountains Wildlife Research Centre and the University of Dar es Salaam. Juan Escós provided computer facilities and developed software for fractal analyses. Field research presented here conducted in 1990–91 was generously supported by grants from the Monbusho International Scientific Research Program to T. Nishida (No. 63043017). During the write-up and analysis, M. A. Huffman was generously supported by a Center of Excellence Research Fellowship at the Primate Research Institute, Kyoto University.

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Received: March 15, 1999

Initial acceptance: May 20, 1999

Final acceptance June 18, 1999 (W. Wickler)

第4章 サルの薬膳料理

マイケル・A・ハフマン／小清水弘一／大東 肇

霊長類は本来は有害な二次代謝産物の豊富な植物を採食することにより、寄生虫感染症をコントロールし、寄生虫の引き起こす病気の症状をやわらげるなどの薬効を得ていることが実証されつつある。さらに、自己治療行動に使う植物の選択基準は類人猿の間で共通している。現地の人の用いる薬用植物と類人猿の用いる薬用植物にはどの程度の類似があるのだろうか。類人猿の薬用植物利用の中に人類の医療行為のルーツを探る。

霊長類は植物を食べてそれを栄養にしているが、植物体には栄養以外の成分も含まれる。種子や果実は、動物に運んでもらって散布されるケースがあるから、植物は動物を惹きつけるための工夫をする。逆に、自分が投資してきた体の構成要素を動物に食べられると損失であるから、植物はそれに対して防衛する。植物が化学物質をつくって防衛する場合、毒物をつくって食べられなくする場合や、消化阻害物質をつくることが知られている。このような防衛的目的でつくられる物質は、植物のつくり出す物質のなかでは二次代謝産物であり、アルカロイドやタンニンを含むフェノールがおもな化学物質である。このような化合物は霊長類にとって障害になるから、いかにそれをとらないように採食するかというのが食物選択の重要な課題であった。ところが、私たちは、チンパンジーの観察で、かれらがこのような障害物質を逆に積極的に食べる事実を発見した。これらの採食は、毒をもって寄生虫感染症の制御やその二次的病徴の治癒を引き起こしていることを示した。

この発見は、他の動物でも自己治療行動をしているのではないかという研究に発展している。自己治療行動に使う植物の選択基準は、類人猿の間で類似しているだけではなく、ヒトの民間治療薬として利用される植物とも類似した選択が見られる。ヒトとチンパンジーが、類似した疾病に共通の植物で治療をすることは、人類の医療行為のルーツの古さを示唆する。さらに、通常の栄養補給を目的として採食されるものにも、薬効を含むものがあることがわかった。サルの採食行動に見られる薬膳料理的な発想が人類の進化過程に大きな役割を果たしたと指摘できる。

本章の目的は、現在得られているアフリカ大型類人猿の間接的・直接的自己治療についての裏づけをレビューし、今後の調査研究の基本的ガイドラインを提供すること、さらに今後この知識を人間の日常の食生活にどう活用していくかを探ることにある。

一　大型類人猿の自己治療行動

アフリカの大型類人猿の自己治療行動には、枝の髄から苦い汁をしがみだして飲み込む行動と葉の呑み込み行動の二つのタイプがあることが示されている[70]。本章では、おもにマハレのチンパンジーに焦点をあて、その自己治療行動を詳しく論ずることにする。

❶　茎の髄の苦汁摂取行動の生態化学

Vernonia amygdalina（キク科・ヤンバルヒゴタイ属）の若い茎から苦い汁を摂取するとき、マハレのチンパンジーは外部の樹皮と葉を取り除いて、露出した内部だけをしがみ、そこから浸出する苦い髄液だけを飲むのである（写真4-1）。一回に摂取する髄部はかなり小さく、直径一センチメートル、長さ五から一二〇センチメートル位である。量にもよるが採食時間は一から八分である[70]。

マハレでの *V. amygdalina* の苦汁摂取行動は、六月と一〇月（乾季後期）を除くすべての月に観察されており、年中採食可能である[71]。しかし頻度からみれば、*V. amygdalina* の採食はまれであり、非常に季節性が強い。苦汁摂取行動はおもに雨季に入った一一月から二月に観察され、一二月から一月にかけて最も高頻度で観察されている。これは、以下に述べる、寄生虫の動態によく対応している。

写真 4-1　*Vernonia amygdalina* の苦い髄部吸い込み行動（上）と *Aspilia mossambicensis* の葉の呑み込み行動（下）を行うチンパンジー．（写真マイケル・ハフマン）

三年にわたるマハレのチンパンジーの腸内寄生虫感染度の研究によれば、腸結節虫（*Oesophagostomum stephanostomum*）に感染した個体の発症率は雨季に上昇するが、他の線虫では違う（図4-1）。腸結節虫感染症は鞭虫（*Trichuris trichiura*）や糞線虫（*Strongyloides fulleborni*）に比べ、苦汁摂取行動との深い関連性が認められる。[75]

苦汁摂取行動の詳細な観察から、この行動をした個体は病気（下痢・倦怠感・線虫感染など）だと推察された。また病気の二個体を追跡調査した結果、苦い髄部の苦汁摂取行動後、二〇から二四時間以内に症状が回復していることが確認さ

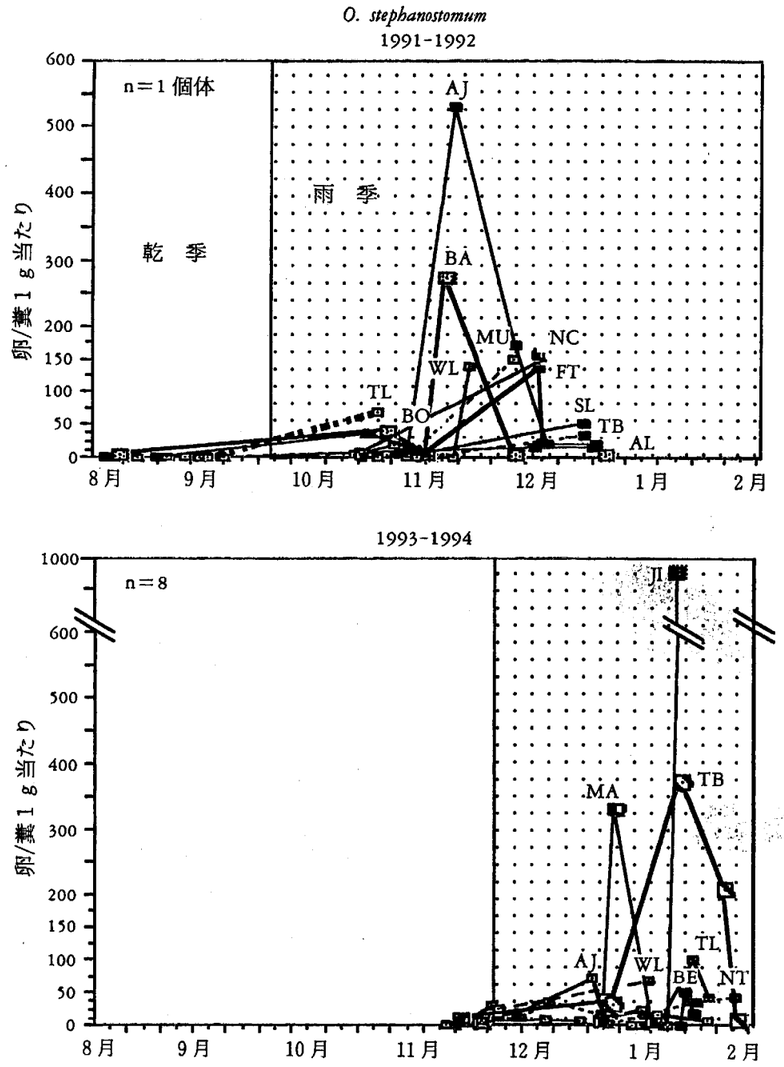
れている。寄生虫感染の程度を糞便一グラム中の寄生虫卵数（EPG）で表すが、苦い髄部の吸い込み後、腸結節虫は二〇時間以内に糞一グラム中一三〇卵から一五卵へと減少することを私たちは確かめた。しかし併発していた鞭虫感染症の糞便ではこのような減少は認められなかった。[72] 同じ時期に観察された個体のほとんどで腸結節虫のEPGが徐々に増加した。雨季はじめのEPG価の増加は、腸結節虫の再感染度の増加を反映していると考えられる（図4-1）。

若い枝の髄から苦い汁をしがみだして飲み込む行動（髄の苦汁摂取行動）は、腸内線虫感染の制御と腹痛の薬理的治療に効果的だと推察した。私たちはチンパンジーの髄の苦汁摂取行動に薬効があるという仮説を提唱するため、明らかに病気とみられるマハレのチンパンジーによる *V. amygdalina* の採食場面の詳細な観察をし、次に、寄生虫学的、植物化学的に分析した。[71][72][75]

V. amygdalina は熱帯アフリカに広く分布している植物である。この他の種のベルノニアの苦汁摂取行動は、タンザニアのゴンベ（*V. colorata*）やカフジビエガ（*V. hochstetteri, V. kirungae*）の各地で観察されている。また、象牙海岸のタイの森では、*Paliouta hirsuta*（ツユクサ科）、*Emremosphath macrocarpa*（ヤシ科）などの苦汁摂取行動が時々観察されている。[70]

❷ 葉の呑み込み行動の行動生態学

葉の呑み込み行動はゴンベとマハレのチンパンジーで最初に記録された。[207] ランガムと西田は、採食された *Aspilia mossambicensis, A. pluriseta, A. rudis*（キク科）の葉が未消化のまま糞便中に排泄されていることに気づき、葉の呑み込み行動は栄養補給のためではないらしいことに注目したのである。その後ロドリゲスら[196]は、アスピリアを噛まずに呑み込むという一風変わった採食方法はチンパンジーが高度な薬的利用法をしているのではないかと示唆した。これにより、他の類人猿



ジーの腸結節虫 *Oesophagotomum stephanosotomum* と *Trichuris trichiura* の個体感染

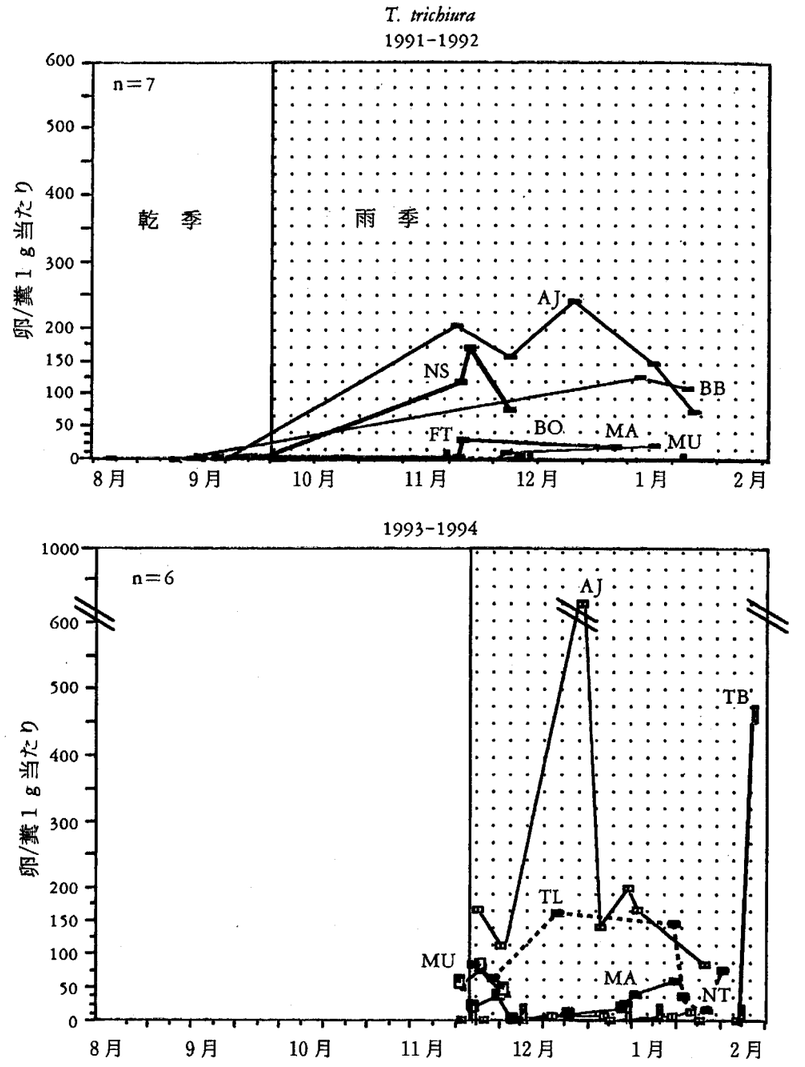


図 4-1　マハレで 1991～1992 年，1993～1994 年に追跡調査したチンパンジーの腸結節虫 *Oesophagotomum stephanosotomum* と *Trichuris trichiura* の個体感染度（卵/糞 1g 当たり）の季節的変動．

にも同様な採食方法がみられるのではないかと野外研究者たちの関心を集めることになった。しかし、その後ロドリゲスらが提示した「アスピリアが含有するチアルブリンAによる殺線虫仮説」[107]は否定されるようになった[74][100]。一九九七年一月一日までにアフリカの一〇カ所の調査地で、チンパンジー九集団とボノボ・ヒガシローランドゴリラの各一集団による二〇種の植物の葉の呑み込み行動が観察されている（表4-1、巻頭の地図も参照）。この行動に選択される植物は多種多様だが（草本・つる・低木・樹木など）、これらに共通した特徴は葉の表面がザラザラして毛状突起があることだ。葉の先端の半分を口のなかにゆっくりと入れ、舌・くちびる・上あごで丸め、やがて一枚一枚呑み込む。一度の採食で一枚から一〇〇枚を呑み込む。苦汁摂取行動と同じく葉の呑み込み行動もまた非常にまれな行動である。

アスピリアの葉はゴンベやマハレでは一年中採取できるが、その採食行動は雨季に入り（一一月～五月）多く観察されている。ピーク時は一月と二月でその他の月の一〇～一二倍の高頻度で観察されている[20]。これはマハレでの髄の苦汁摂取行動のパターンとよく似ている。アスピリア以外の九種の植物の葉も類似の方法で呑み込まれ、やはり雨季に多く観察されている[75]。

ハフマンは一九九三年一二月から一九九四年二月にかけての三ケ月にわたり、行動様式・健康状態のデータ収集とともに葉の呑み込み行動を直接観察した。詳しく観察できた八頭のチンパンジーのうち、七頭は、葉を呑み込んだときに下痢・倦怠感の兆候や腹痛の気配が認められた[74]。直接観察あるいは葉を含んだ糞便の間接的証拠によって確認された一二例の葉の呑み込み行動のうち、八三パーセントに線虫感染症が認められた[74][75]。普段排泄される糞便中に寄生虫の成虫がいることはまれだが（三パーセント、九／二五四）、調査期間中にはこうした成虫が見られたが、このような、成虫を排出する個体は倦怠感や下痢の症状を表す個体にかぎられていた。これらの成虫は腸結節虫であった。

葉の呑み込み行動と腸結節虫駆除との間には強い関連性が認められた。一九九三年から一九九四年には九個の糞便

（N＝二五四）のうち六個に *A. massambicensis* や *Trema orientalis*（ニレ科・ウラジロエノキ属）または *Aneilema aequinoctiale*（ツユクサ科）の葉が未消化のまま認められた。一個の糞便中に二匹の腸結節虫が、*A. aequinoctiale* の葉の表面の毛状突起にしっかりと付着しているのが認められた。糞便中の未消化の葉と腸結節虫の出現率は統計的に有意に相関していた（Fisher's exact test, two sided, P＝0.0001）[74]。残りの腸結節虫のほとんどは丸められた葉のなかに入っていた。こうして、糞中に発見した結節虫のすべてはまだ生存しており動いていた。たとえ数日間、腸結節虫を糞・葉といっしょに保管しておいても成虫は変わりなく生き動きつづけることから、化学的な殺線虫作用ではなく葉の物理的作用によって腸結節虫を駆除することが葉の呑み込み行動における主たるメカニズムではないか、との仮説を私たちは提唱している[74]。

最近になって、そのメカニズムについて新たな視点が得られている。一九九三から一九九四年調査で得られたデータを再分析した結果、マハレのチンパンジーが呑み込む葉は五から六時間で消化管通過を通過し、未消化のまま排泄されることがわかった。これは通常の消化時間に比べ四分の一かそれ以下である。類人猿の葉の呑み込み行動でハフマンとジュディス・ケイトン（オーストラリア国立大学、シドニー）は、葉の表面のザラザラとした毛状突起が腸管を刺激し、その結果、消化時間が短縮され、物理的に腸結節虫を駆除しやすくするのではないかとの仮説をたてている。すなわち、表面に消化しにくい物質でできている毛状突起がある葉は朝の空腹時に食べることで、腸の粘膜に付着している腸結節虫が体外に排泄されやすくなるのだろう。

以上のように、葉の呑み込み行動は腸内寄生虫の駆除を通じた腸結節虫感染症の制御や、その感染症による痛みの緩和に効果があると考えられている。

近年、多くの観察データが次々と報告されるようになり、動物の自己治療に関する研究にいっそうはずみがついてきた[70]。こうした研究では、動物が自己治療のために植物二次代謝産物またはその他の非栄養的な物質を利用するというこ

Trema orientalis (L) Blume syn. *T. quineensis*	×					
Celtis adorfi-frederici Engl.						×
MELASTOMATACEAE						
Melastomastrum capitatum Vahl A. and R. Fernandes	×					
Tristemma coronatum Benth.				×		
Dichaetanthera africana (Hook. f.) Jac.-Fel. l.c. (syn. *Sakersia africana*)				×		
CONVOLVULACEAE						
Ipomoea involucrata P. Beauv.		×				
CUCURBITACEAE						
Lagenaria abyssinica (Hook. F.) C. Jeffrey		×				
Adenopus abyssinicus Hook. F.		×				
*Peponium*sp.		×				
ICACINACEAE						
Polycephalium capitatum (Baill.)					×	×
EUPHORBIACEAE						
Maniophyton fulvum Mull. Arg			×	×	×	
Cyperaceae sp.					×	
未同定					×	×
					(2 spp.)	
N＝30．（未同定 3 spp.）	10	3	3	5	1	1	6	1	6

1）調査地とそこで利用される植物についての情報源に関しては，文献

2）Pts: *Pan troglodytes schweinfurthii*（ヒガシチンパンジー），Ptt.: *P.t. troglod*
ボ），Ggg: *Gorilla gorilla graueri*（ヒガシローランドゴリラ）

表 4-1 アフリカ大型類人

み込み行動に利用する植物

地域	東部			中央部			西部アフリカ		
国	タンザニア		ウ	旧ザイール		コンゴ	象牙海岸		ギニア
調査地[1]	マハレ	ゴンベ	キバレ	カフジビエガ	ワンバ	ンドキ	タイ	ニンバ	ボッソウ
類人猿の種[2]	(Pts)	(Pts)	(Pts)	(Ggg, Pts)	(Pp)	(Ptt)	(Ptv)	(Ptv)	(Ptv)
科 種									
COMPOSITAE									
Aspilia mossambicensis (Oliv.)	×								
A. pluriseta (O. Hoffm.) Wild		×							
A. rudis Oliv. and Hiern		×							
MALVACEAE									
Hibiscus aponeurus Sprague and Hutch	×	×							
VERBENACEAE									
Lippia plicata Baker	×								
COMMELINACEAE									
Commelina diffusa Burm. f.	×								
C. benghalensis Linn.	×								
C. cecilae C. B. Clarke				×, ×					
Aneilema aequinoctiale (P. Beauv.) Loudon	×		×						
A. nyasense C. B. Clarke	×								
RUBIACEAE									
Rubia cordifolia L.			×						
GRAMINEAE									
Hyparrhenia cymbaria (Linn.) Stapf			×						
MORACEAE									
Ficus exasperata Vahl	×								×
F. mucuso Ficalho									×
Antiaris africana Engl.									×
ULMACEAE									

二　大型類人猿の日常食の生態化学的考察

この節では、大形類人猿が日常的に摂取する植物の薬効作用について検討する。

❶ 果実と葉に含まれる二次代謝産物

チンパンジー・ボノボ・ローランドゴリラなどは概して果実食者であり、多種多様な葉・髄部・種子・花・樹皮・樹液などを採食している。多くの二次代謝産物が植物のこれらの部位から分離されてきた。無機物質や二次代謝産物は草食動物に対する植物の防衛最前線であると考えられている[67]。これら二次代謝産物は採食者にとって有毒か、もしくは消化力を低下させたり食欲を減退させたりすることにより摂取されにくくする物質だが、大型類人猿の日常食には多くの二次代謝産物が含まれている（表4-2）。

西ウガンダ、キバレのカニャワラ・グループのチンパンジーでは、*Phytolacca dodecandra*（ヤマゴボウ科ヤマゴボウ属）の果実を多量に高頻度で採食している（ランガムとイサビリエ・バースタによる私信）。その実は苦味があり少なくとも四種の毒性トリテルペンサポニンの濃縮物質を含んでおり、わずか二グラムでマウスとラットの致死量となる。最高濃度の毒性は果実に含まれているが、これら化合物は住血吸虫の中間宿主である巻貝を殺す作用があり、現在アメリカで殺巻貝剤として開発中である。その他の生物活性としては、抗ウイルス・抗菌・避妊・殺精子・胚毒性作用などが挙げられる。

とが前提となっている。自己治療をするかどうかは、個体の経験によって、また部分的には本能・食欲・あるいは通常の採食行動の副産物によって意識的に決まる。

自己治療を理解するうえでの難点であり今後の研究課題の一つは、二次代謝産物の豊富な植物を栄養補給の目的に摂取して間接的に薬効を得る場合と、薬効だけを期待して採食すると思われる場合を区別することである。人間の社会でも食用と薬用植物の区別は、元来あまり明確ではなかった。その適切な事例として、アジア各地の日常食にみられるスパイス・薬味・ショウガ・各種ハーブなどが挙げられる。これらのなかには発がん抑制作用、さらにはウイルス抑制作用がある[134]。人間側から見ればこれはまるで薬膳料理のようなものだ。

寄生虫は多くの病気を誘発し、個体の行動全般や繁殖能力に影響をおよぼす。したがってこれらの悪影響や感染した場合の宿主の反応は、長い進化の産物であることは間違いない。霊長類やその他の哺乳類が偶然採食した植物二次代謝産物が寄生虫駆除に効果があるという必要性は非常に大きいはずである。寄生虫感染症が宿主へ与える影響を抑制する可能性は、かなり以前から示唆されていた[107]。

しかしアフリカの大型類人猿についての最近の調査結果は、かれらが偶然ではなく薬効を期待して特定の植物を摂取していることを示している。この観察は、ほ乳動物の自己治療に関する現時点での最も決定的な状況証拠を提供している。類似した病状の場合、ヒトとチンパンジーは同じ植物を選択するが、これはおそらく両者が系統的に最も近縁なためだろう[73]。大型類人猿から初期人類、現生人類にいたるまでの医療行為の進化を考えるうえで、自己治療行動の観察から導きだされる研究結果は非常に重要であろう。

自己治療についていままでに得られた詳しい情報のなかでは、アフリカ大型類人猿についての情報が最も多いが、類人猿以外の霊長類とその他の哺乳類にも自己治療行動は見られるものと推察される。

表 4-2　一般的な植物二次代謝産物とそれらが動物に与える影響

化合物のタイプ	薬理効果（特記事項）
テルペノイド，アルイカロイド	イオンチャンネルの修飾（高毒性）
イソキノリンアルカロイド	DNA に挿入，受容体と相互作用，痙攣作用（毒性があり，苦みを呈する）
キノリジンアルカロイド	ACH 受容体に結合（毒性があり，苦みを呈する）
トロパンアリカロイド	ACH 受容体の阻害（高毒性）
ピロリジジンアロカロイド	変異原性，発癌性（肝臓毒）
シアン配糖体	呼吸阻害
アルジアック配糖体	Na＋/K＋ -ATPase 阻害（高毒性）
テルペン	利尿作用（苦み）
揮発性テルペン	抗菌性，刺激性
揮発性モノテルペン	抗菌性（芳香性）
サポニン，アミン	生体膜に対し界面活性（苦み）
トリテルペン，サポニン	生体膜に対し界面活性（苦み，催吐性）
セスキキペルペン，ピロリジジン	変異原性，発癌性，刺激性（細胞毒，肝臓毒）
コンバラトキシン	Na＋/K＋ -ATPase 阻害（高毒性，苦み）
アントラキノン	便通作用（毒性）
フェノール性物質	収斂（しゅうれん）性，抗消化性
セルロース，ヘミセルロース，リグニン，シリカ	非消化性

野生のショウガの髄部や果実はアフリカ全土のチンパンジー、ボノボ、ゴリラが採食している。ジョン・ベリー（コーネル大学、生物学部）は南西部ウガンダのブウィンディにおいて、マウンテンゴリラ *Gorilla gorilla beringei* の日常食を生態化学的に研究しているが、その一環として野生ショウガの一種 *Aframomum sanguineum* の果肉の生物活性についての調査を進めている。果肉と種子の抽出物の分析評価によれば、重要な抗微生物活性を有している。またこの実は、バクテリア感染や真菌感染の治療薬としてさらには、駆虫剤としてブウィンディの市場や路端で市販されている（ジョン・ベリーによる私信）。

北部コンゴのンドキの森で、*Thomandersia laurifolia*（キツネノマゴ科）の若葉の先端をニシ・ローランドゴリラ（*G. g. gorilla*）が噛むことがまれにある（黒田、モクム、西原による私信）。黒田未寿（滋賀県立大学）らによれば、原住民はこの若葉を抗寄生虫薬や解熱剤として利用しているのである。これらの葉の抽出物

からわずかではあるが抗住血吸虫作用が認められている。

❷ 栄養の乏しい樹皮と木部

樹皮と木部は繊維質、木質に富むが、時には毒性もあり、消化はあまりよくなく栄養源としても乏しい。[210] それにもかかわらず、チンパンジーやゴリラが多くの種の樹皮や木部を頻繁に採食することはよく知られているが、日常食のなかで樹皮がいったいどのような役割を果たしているかは、まだほとんど明らかにされていない。アフリカの民俗生薬学の文献によれば、これらの植物のなかには重要な薬理効果をもつものもあり、今後の類人猿の行動学的・植物化学的な調査にとって新しい研究材料となりうる。マハレのチンパンジーは *Pycnanthus angolensis*（ニクズク科・薬味のナツメグの仲間）を摂取するが、西アフリカの人々も、下剤、消化剤、吐剤、歯痛止めなどとして利用している。マハレのチンパンジーが *Grewia platyclada*（シナノキ科）の樹皮をむいて噛んでいることが時々観察されるが、現地人もこれを胃痛の治療薬として噛んでいる。一方、ゴンベのチンパンジーは *Entada abyssinica*（マメ科・モダマ属）の樹皮を時々食べるが、ガーナの人々はこれを下痢または吐剤として利用している。ギニア、ボッソウのチンパンジーは *Gongronema latifolium*（ガガイモ科）の樹皮を食べるが、これは非常に苦い。西アフリカの人々は、この茎をさしこみ痛時の下剤、腹痛、腸内寄生虫感染関連の症状などの治療に利用している。マハレのチンパンジーは *Erythrina abyssinica*（マメ科）の樹皮を時々食べるが、この種の樹皮の抽出物からは強い殺マラリア原虫と抗住血吸虫活性が認められている。[76]

マハレのチンパンジーが食用とする植物が、寄生虫駆除に効果があるかどうかを検討するため、彼らが採食すると報告されている植物についてアフリカの民俗生薬文献を参考にし、文献調査が実施された。

三　類人猿自己治療植物の薬理的民間利用法

❶　苦汁摂取行動

アフリカの多くの民族は、マハレのチンパンジーも利用した *V. amygdalina* の抽出液を、マラリア、住血吸虫感染症・赤痢アメーバ・その他腸内寄生虫症や胃痛の治療薬として利用している。詳しく観察されたマハレMグループの二頭のチンパンジーは、髄の苦汁摂取後二〇〜二四時間で回復したことが認められた。これは現地人ワトングウエが *V. amygdalina* の冷たい抽出液を寄生虫感染症・下痢・胃痛などの治療に利用するときに、改善が得られるまでにかかった時間と一致している。[71][72]

ゴンベ・カフジビエガ・タイの森でチンパンジーが採食する苦い髄部のある別の植物のなかには、民間生薬として薬理的な特徴を多くもっているものもある。例えばゴンベのチンパンジーがたまに採食する *V. colorata* は、*V. amygdalina* に極めて近縁な種である。両者とも、アフリカの伝統的な治療薬として利用されている。この二種は民間の分類では区別されておらず、薬効も同じとされている。一方、*V. hochstetteri* の髄部にはアルカロイドが含まれている。*P. hirsuta* や *E. macrocarpa* は西アフリカでは、腹痛・腸炎・抗菌剤・鎮痛剤・また性病に対する治療薬としても利用されている。*P. hirsuta* には住吸血虫の中間宿主である巻貝を殺す作用があることも報告されている。

私たちは、チンパンジーが利用したのを直接観察した *V. amygdalina* 数本を化学分析した結果、生理活性物質にはおも

本分析にあたっては、一九二種の食用植物のなかから、栽培種ではなく学名まで同定されている一七二種を検索した。ある植物は複数の民間生薬として利用される一方、一七二種のうち二五パーセントに当たる四三種は寄生虫や胃腸病の治療薬として使用されていることがわかった。チンパンジーはこの四三種すべてをこのような薬理効果が得られるようなやり方で食べているとはかぎらないかもしれない。だが、一六種の植物から採食される部位の三二パーセント（二〇／六三）は、腸内寄生虫症や胃腸病の治療薬として人間が利用している採食部位と一致している。[76]この一六種は興味深いことに、マハレのチンパンジーが雨季に際立って多く採食し、しかも腸結節虫感染症（oesophagostomiasis）の制御に利用していると考えられる次節で紹介する植物種と同じである。東南アジアのオランウータンについては自己治療の全貌がまだ明らかにされていないが、多くの植物の樹皮を採食することが知られている。そのほとんどが形成層である。樹皮を噛みしがむだけで、その繊維質は食べられることなく吐き出されることが多い。

以上の調査の概略から、大型類人猿の日常食に潜在する薬理的活性の多様性がわかるだろう。大型類人猿が摂取する植物がどんな効果をもたらしているのか全容はまだ明らかではないが、栄養補給だけのために摂取していると判断するにはまだ早すぎるのは明白である。今後、大型類人猿の日常食を生態化学的にさらに追求していけば、野生植物の摂取が病気の予防手段となることについての私たちの理解を深めることができるだろうし、新たな天然代謝産物を見出すよい手がかりともなろう。類人猿が日常食として摂取する天然植物に含まれる物質の活性スクリーニングをすることが、潜在する抗寄生虫活性を追求するための効果的な方法の一つであることが明白となってきた。

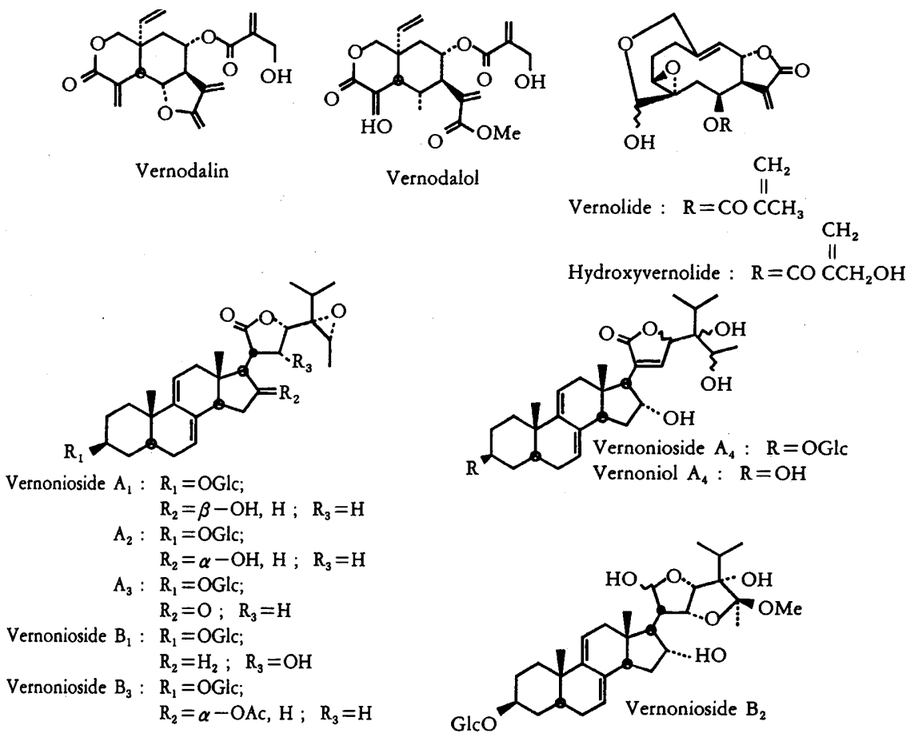


図 4-2　Vernonia amygdalina から単離されたステロイド配糖体とセスキテルペンラクトン関連化合物の化学構造。

に二種類あることを実証した。すなわち、今日までに計四種のセスキテルペンラクトン（vernodalin, vernolide, hydroxyvernolide, vernodalol）、七種の新しいスチグマスタン型のステロイド配糖体（vernonioside A1-A4, B1-B3）と二種のアグリコン（vernoniol A1, B1）が分離されている。

民間生薬の文献から *V. amygdalina* や *V. colorata*、その他多くのベルノニア属植物には、駆虫・抗アメーバ赤痢・抗腫瘍・抗生理活性物質などでよく知られているセスキテルペンラクトンが存在していることがわかっている。乾燥植物体（葉）のメタノール抽出から、小清水らにより[15]腫瘍発生の抑制作用と免疫抑制作用のあることが判明した。

髄部に最も豊富に見られるステロイド配糖体（vernonioside, 2B1）とセスキテルペ

ンラクトン（vernodalin）の抗住血吸虫作用についての in vitro 試験によれば、成虫の運動阻害活性と成虫雌の産卵抑制作用のあることが認められた。この結果は、マハレのオトナ雌のチンパンジーの例において *V. amygdalina* 髄部採食後二〇時間で、腸結節虫ＥＰＧレベルの減少が観察されたという事実と一致している。

葉や樹皮に豊富に含まれている vernodalin は強い毒性を示すが髄部にはごくわずかしか含まれていない。なぜチンパンジーが通常は葉や樹皮を避けステロイド配糖体やアグリコンが圧倒的に豊富な髄部を選んで食べるのかという問いに対して、この事実は明確な解答を与えている。[82]

❷ 葉の呑み込み行動

呑み込み行動により採食される植物について、その二次代謝産物が寄生虫駆除に特別な役割を果たしていると提唱できる十分な化学的・薬理学的証拠は、現在のところ得られていない。すでに述べた物理的メカニズムは、呑み込み行動植物の寄生虫駆除における種々の観察結果をうまく説明できる、よいモデルと考えられる。しかしながら、化学的効果による寄生虫駆除もまだ捨てきれないのは以下のような事実もあるからである。すなわち、最近五カ所の調査地で類人猿が飲み込んだとされる五属五種の葉（*Maniophyton fulvum, Ipomea involucrata, T. orientalis, Lippia pliciata* と *Lagenaria abyssinica*：学名などについては、本章の付録参照）の抗住血吸虫（*Schistosoma japonica*）と殺マラリア活性を in vitro で検討した。[76] その結果、五種のうち四種の抽出物中には一〇〇マイクログラム／ミリリットルの濃度で住血吸虫の産卵活動に対する阻害活性が認められた。また殺マラリア活性も認めれている。化学的効果の説明として、消化器官を通過する過程で葉に存在する成分が腸粘膜壁への線虫の付着能力を減退させ、ザラザラした表面をもつ葉によりくっつきやすくさせ、効率的に体外へ

また、腸内寄生虫だけが唯一の病気の原因ではなく、他の原因も検証する必要がある。しかし野外調査でできることには限度があり、自己治療行動の予想される影響を十分把握するためには、動物や植物に関する各研究分野（獣医学・薬理学・天然代謝物化学など）の多彩な研究者の協力が不可欠である。マハレで行われたC. H. I. M. P. P. Group (Chemoethology of Hominoid Interaction with Medicinal Plants and Parasites) による学際的研究は、各専門分野での研究がいかに効果的に進められてきたかを示すよい例である。[69]

自己治療行動を野外で調査するときの最大の制約は、（一）行動がいつ起こるか予測できないこと、（二）病気の個体の密着追跡調査を確実に遂行できるとはかぎらないこと、（三）実験操作上の制限があること、の三点である。自己治療行動の仮説から得られる考察を検証していくためには、これらの制約を取り除かなければならない。例えば飼育ザルに安全な薬用植物を与えることにより、彼らが薬草を選択する際の基準を評価し、個体が自己治療をどのように獲得し、それがグループにどう伝えられて行くのかを明らかにすることができるかもしれない。動物園の霊長類やその他の動物の自己治療行動の潜在能力を探ることにより、野生動物に何が起きているのかをよりよく把握できると期待される。さらにこのことは、環境エンリッチメントや健康維持の包括的なアプローチとして、飼育動物にとっても有益だろう。

❷ 飼育動物のための薬的ハーブと環境エンリッチメント

飼育サルに薬としての効果をもつハーブを導入するという先駆的計画が、一九八五年からオランダのアペヌール動物園で進められている。動物園内に自由移動・採食状態で飼われているウーリーザルの集団で発生しがちな疾病のうちおもなものをピックアップしたあと、小さなハーブ園を設けた。そこには様々な薬理効果があるとされているハーブを導

と排出されるのではないかと考えられる。[74] 物理的効果と相まった化学的効果仮説の検証には、ベルノニアで展開された方法と同様、活性を示す成分の単離、同定を通した今後の研究を待たねばならない。

四 今後の研究の方向性と実際の応用

❶ 基本的ガイドラインと予見

以上に述べた証拠から、類人猿は腸内寄生虫を制御する目的で様々な適応行動をとることが示唆された。アフリカ大型類人猿の自己治療行動に関する現在の仮説を支持する詳細な証拠のほとんどは、彼らが寄生虫感染度の変化に応じて対処方法を変えていることに示されている。このモデルは、季節的繁殖をする寄生虫に感染した他の多くの霊長類にもあてはまるだろう。

寄生虫感染度の変動を、集団レベルでなく、個体レベルで体系的に通年追跡調査することは、主要な寄生虫が宿主に与える影響の高まる時期を判定する一つの有力な手がかりとなる。いろいろな行動（休息時間・歩行時間・食事時間など）を詳細に分析し、集団の健康状態を長期に追跡調査し、健康状態を表す一般的な症状（下痢・せき・鼻水など）を体系的に検査することは、発病時の病気判定に必要である。また、提起されている自己治療行動の機能と効果だけでなく、その病気の直接の影響を把握するためにも必要だと考えている。これらの調査手続きを他の霊長類の野外調査手続きに取り込むことは十分可能である。

タンザニア・ウガンダ・ケニアの共同研究者と、様々な寄生虫感染に対する、これらの植物の効果の検証にはげんでいる。この研究の一環として、アフリカ固有で安く手に入り、自給可能な植物を抗寄生虫物質として利用する可能性も探っていく予定である。

❹ 今後への期待

類人猿以外の霊長類の自己治療行動についても、野外と実験室の両方で研究を進めることが強く望まれる。本章で述べたように、疑問に対する答えは必ず次の疑問を産み出す。多くの野外研究者が類似した自己治療行動を探しているので、そうした行動が実際に見出されるのもそう遠くないだろう。その結果、現在提起されている疑問にも一つ一つ答えが出されいくだろう。別の形であっても、自己治療行動は大型類人猿だけでなくサルや原猿類にもみられるものと考えられる。自己治療行動は明らかに適応的に重要なため、動物界に広く存在していると推察される。ある集団において動物の健康や生存そのものへの直接の脅威はいったい何なのか、そしてその種はその脅威にどんな方法でどう対処しているのかを明らかにすることが、今後の研究課題である。

アフリカ大型類人猿の間では自己治療行動に使う植物の選択基準が酷似している。さらに、ヒトとチンパンジーが類似した疾病には共通の植物で治療をする。これらは人類の医療行為のルーツの古さを示唆する。この点で、初期人類は現生類人猿と現生人類の植物選択基準と類似したものをすでに獲得していたと考えられる。化石からは食事行動と食事内容の微細な点まで裏づける直接の証拠は見出せないが、初期人類が現生の類人猿と同程度までの自己治療行動をすでに獲得していただろうことは容易に想像できる。

入した。アメリカのコロラド州のデンバー動物園でも園芸担当のメルレ・ムーア氏によってこれと同様な試みが進められている。これらのハーブが動物の健康にどのような効能を実際に与えているかについては、いまのところ臨床的に評価されていない。しかしこうした試みは、環境と食事内容のエンリッチメントのための斬新な方法を示している。

以上に述べた試みは、薬草利用という霊長類による潜在的学習能力を研究する最適な方法である。飼育霊長類に共通して見られるストレスやその他の健康問題解消のためのハーブ採食行動を臨床的および行動学的に評価する研究でもある。こうした研究は世界各地の動物園や研究施設において、地域特有の自給できる植物の利用価値や安全性を確かめながら進められ、動物福祉面でもっと調和した健康維持と動物環境エンリッチメントの方法を開発することが望ましい。

❸ 発展途上国における家畜用治療薬という自給資源

自己治療行動研究の将来の方向性の一つは、いままでに得られた食用・薬用植物についての知識を応用し、それらを医学と獣医学に活用することである。腸結節虫感染症は霊長類とブタ・ヒツジ・ウシなどの家畜に共通して見られるが、時にはヒトにも認められる。現在では家畜の治療薬として各種の販売駆虫剤が手に入るが、寄生虫による薬剤耐性がいっそう強くなっているのが現状である。発展途上国の貧しい家庭・小規模の家畜産業・動物園にとっては駆虫剤がとても買えないほど高いために、たとえ時には購入できたとしても実用的とはとても言えない。

したがって、民俗生薬から得られる天然化合物を治療に利用するという新しい方法への関心が最近高まってきている。大型類人猿における自己治療行動の研究によって、自然界やそれから単離される化合物がヒト・家畜・飼育動物などの寄生虫駆除にも効果を発揮すると期待される。アフリカでの調査結果を基に、私たちは日本・デンマーク・フランス・

Afromomum sanguineum (K. Schum.) K. Schum. ZINGIBERACEAE　ショウガ科
Aspilia (syn. *Wedilia*) *mossambicensis* (Oliv.) ASTERACEAE　キク科
Aspilia pluriseta (O. Hoffm.) Wild ASTERACEAE　キク科
Aspilia rudis Oliv. Hieren ASTERACEAE　キク科
Emremospath macrocarpa (Mann & Wendl.) Wendl. PALMAE　ヤシ科
Entada abyssinica Steud. ex A. Rich MIMOSACEAE　ネムノキ科（マメ科）・モダマ属
Erythrina abyssinica DC. PAPILIONACEAE　マメ科
Gongronema latifolium Benth. ASCLEPIADACEAE　ガガイモ科
Grewia platyclada K. Schum TILIACEAE　シナノキ科
Ipomea involucrata P. Beauve CONVOLVULACEAE　ヒルガオ科・サツマイモ属
Lagenaria abyssinica CUCURBITACEAE　ウリ科
Lippia plicata Baker VERBENACEAE　クマツズラ科・イワダレソウ属
Maniophyton fulvum Mull. Arg EUPHORBIACEAE　トウダイグサ科
Paliosota hirsuta (Thumb.) K. Schum COMMELINACEAE　ツユクサ科
Phytolacca dodecandra L Herit PHYTOLACCACEAE　ヤマゴボウ科・ヤマゴボウ属
Pycnanthus angolensis (Welw.) Warb. MYRISTICACEAE　ニクズク科
Thomandersia laurifolia (T. Anders. ex Benth.) Baill ACANTHACEAE　キツネノマゴ科
Trema orientalis (L) Blume syn. *T. guineensis* ULMACEAE　ニレ科・ウラジロエノキ属
Vernonia amygdalina Del. ASTERACEAE　キク科・ヤンバルヒゴタイ属
Vernonia hochstetteri Schi-Bip. ASTERACEAE　キク科・ヤンバルヒゴタイ属
Vernonia kirungae Rob. E. Fries ASTERACEAE　キク科・ヤンバルヒゴタイ属

属名，種名，科名，科和名，属和名の順．
日本に同じ属がない場合は科名のみを示している．

霊長類の自己治療研究は、自然界の多様性を表す宿主・寄生虫・植物の複雑な相互作用・霊長類の行動生態学・人類の進化過程など様々な課題を理解するうえで、また一つの斬新な視点を提供するだろう。