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Rodent Biology and Management

Abstracts of papers presented at the International Conference on Rodent
Biology and Management, held at Beijing, China, 5–9 October 1998

*Editors: Zhi-Bin Zhang, Lyn Hinds, Grant Singleton
and Zu-Wang Wang*

Australian Centre for International Agricultural Research
Canberra 1999

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Preface

The International Conference on Rodent Biology and Management (ICRBM) was held in the Beijing Friendship Hotel on 5–9 October 1998. The conference was co-organised by the Institute of Zoology, Chinese Academy of Sciences, and CSIRO Wildlife and Ecology, Australia.

Over 140 presentations were made. The framework of the scientific program of '98 ICRBM detailed in this report was organised by Lyn Hinds, Grant Singleton, Herwig Leirs, Anita Dalakoti and Zhi-Bin Zhang, and finalised through extensive communication with the symposium chairs.

The abstracts of '98 ICRBM are listed in the order of the surname of the first author. The abstracts of participants from non-English speaking countries were modified for readability. No intentional changes to the content were made. The views of the authors of these abstracts are not necessarily those of the editors or the organising committee.

We thank all those who contributed to the successful organisation of the conference. We also thank ACIAR who has generously supported the reprinting of the full set of conference abstracts. We thank Karen Weaver for her editorial assistance.

Editors

Zhi-Bin Zhang Secretary General of '98 ICRBM
Lyn Hinds Co-chairman of '98 ICRBM
Grant Singleton Co-chairman of '98 ICRBM
Zu-Wang Wang Executive Chairman of '98 ICRBM

General Information

'98 ICRBM

The **International Conference on Rodent Biology and Management** ('98 ICRBM) was held in the *Friendship Hotel*, 3 Bai Shi Qiao Road, Beijing 100837, China on 5–9 October 1998.

The conference was organised by:

- Institute of Zoology, Chinese Academy of Sciences
- CSIRO Wildlife and Ecology, Australia

and sponsored by:

- Australian Centre for International Agricultural Research (ACIAR)
- Chinese Academy of Sciences (CAS)
- Chinese Nature Science Foundation (CNSF)
- Cyanamid (China) Co. Ltd
- Tianjing Tianqing Chemicals Co. Ltd
- Longhua Insecticides Co. Ltd
- Zhang Jia Kou Twin Round Kikbo Pharma Co. Ltd
- Kalian Chemical Experimental Factory

with assistance from:

- Animal Ecology Committee, Chinese Ecological Society
- National Key Laboratory of Integrated Pest Management of Insects and Rodents in Agriculture, CAS
- Rodent Control Committee, Chinese Plant Protection Society.

The Organising Committee was:

- Honorary Chairmen: Charles J. Krebs (Canada) and Ru-Yong Sun (China)
- Executive Chairman: Zu-Wang Wang (China)
- Co-chairmen: Grant Singleton and Lyn Hinds (Australia)
- Secretary General: Zhi-Bin Zhang (China)
- Committee Members: Alan Buckle (U.K.), Herwig Leirs (Denmark), Valery Neronov (Russia), Dale Nolte (USA), An-Guo Chen, Zhi Deng, Nai-Chang Fan, Yong Ma, Ji-Ke Liu, Hao-Quan Lu, ChengXin Wang, Wen-Qin Zhong, Wen-Yang Zhou, En-Lin Zhu (China)

The conference aimed to promote rodent management based upon biological and ecological studies. The scientific program included opening and closing ceremonies, plenary presentations, symposium presentations, specialist discussion groups and workshops, and poster sessions.

ICRBM meeting: 4 October 1998

The meeting was chaired by Zhi-Bin Zhang and Grant Singleton. The honorary chairmen, executive chairmen, symposium chairs, plenary chairs, organising committee members and discussion group chairs of ICRBM attended this small meeting.

Opening ceremony: 5 October 1998

Chairs: Grant Singleton and Zhi-Bin Zhang

Keynote speakers: Zu-Wang Wang, CAS-IOZ Director and ICRBM Executive Chairman

Grant Singleton, CSIRO-WE and ICRBM Executive Co-Chairman

Bob Clements, ACIAR Director

Jian-Ji An, Associate Director-General, Bureau of International Cooperation, Chinese Academy of Sciences.

Da-Bao Zhu, Director of Life Sciences Division of the Chinese Natural Sciences Foundation.

Closing ceremony: 9 October 1998

Chairs: Herwig Leirs and Zu-Wang Wang

Keynote speakers: Charles Krebs, ICRBM Honorary Chairman

Ru-Yong Sun, ICRBM Honorary Co-Chairman

John Copland, ACIAR Project Coordinator

Lyn Hinds, CSIRO-WE and ICRBM Executive Co-Chairman

Zhi-Bin Zhang, CAS-IOZ and ICRBM Secretary General

Scientific Program

Symposium A: Population dynamics—including forecasting and managing rodents

Plenary lectures

Charles Krebs* (Canada—invited lecture), Current paradigms of rodent population dynamics—what are we missing?

Zhi-Bin Zhang (People's Republic of China), Rodents in China—population dynamics and management.

Oral presentations

Leirs, H. Populations of African rodents: models and the real world.

Stenseth, N.C. Seasonality and population cycles in small rodents.

Guo, C., Zhang, M.W., Wang, Y., Li, B. and Chen, A.G. The influence of high temperature and migration on reproduction of *Microtus fortis calamorum* in the Dongting Lake area.

Abramson, N.I. and Nadachowski, A. Reconsideration of lemming phylogenetic history with special reference to the origin of *Synaptomys*.

Lushchekina, A.A. and Neronov, V.M. Specific features of the distribution of the great gerbil (*Rhombomys opimus*) in central Asia.

Montague, T. and Choquenot, D. The diet and dynamics of New Zealand's forest-dwelling house mouse (*Mus musculus*) in the Orongorongo Valley.

Wan, X.R., Zhong, W.Q., Wang, M.J. and Wang, G.H. The cohort life table of the Brandt's vole (*Microtus brandtii*) in Inner Mongolian grasslands, China.

Tchabovsky, A., Shilova, S., Neronov, M.V. and Alexandrov, D.Y. Rodent population dynamics under environmental change: is it an ergodic process?

Pech, R., Hood, G., Singleton, G.R. and Brown, P. Models for predicting plagues of house mouse (*Mus domesticus*) in Australia.

Liu, J.K., Su, J.P., Liu, L.K. and Wang, Z.L. Analysis of the effects of predation and food availability on population dynamics of root voles.

Predavec, M. The role of food limitation in irruptions of Australian desert rodents.

Steen, H. and Haydon, D. Can population growth rates vary with the spatial scale at which they are measured?

Tristiani, H., and Murakami, O. Seasonal changes in the population density and reproduction of the rice field rat, *Rattus argentiventer* (Rodentia, Muridae), in West Java.

Wang, Y.Z., Lu, H.Q., Chen, A. and Su, C.D. Forecasting the relationship between population size of the striped hamster and ecological factors.

Poster presentations

Abramson, N.I. Variation, taxonomy and distribution patterns of the genus *Lemmus* in the palaeartic.

* Names of paper presenters are in bold type.

- Chang, W.Y.**, Ning, Z.D., Wang, T.L., Zou, B. and Wang, K.G. Growth and development of the sulfur bellied rat (*Rattus niviventer sacer*).
- Golenishchev, F.N.**, Aksenova, T.G. and Pavlova, N.A. Peculiarities of structure of dental system and morphometric variation in *Lasiopodomys mandarinus* and *L. brandti*.
- Golenishchev, F.N.** and Meyer, M.N. Distribution patterns of two chromosome forms of common vole (*Microtus arvalis* pal.) on the common border of their range.
- Guo X.H.**, Dazhao, S. and Shuzhen, H. Study of seasonal survival rates of populations of *Microtus brandti*.
- Hung, N.Q.**, Singleton, G.R., Quoc, N.V., Hung, N.M., Brown, P. and Lan, L.P. Migration of rodent species in agricultural landscapes in the Vietnam–Cambodia border region.
- Kaetzke, P.** and von Hoist, D. What stops population growth in the wild rabbit (*Oryctolagus cuniculus*)?
- Liu, D.Z.**, Liu, N.F. and Song, Z.M. The environmental effects on the distribution of long-eared jerboas (*Euchoreutes naso*).
- Tupikova, N.V.**, Varshavsky, A.A. and Khliap, L.A. Rodent and pika population of south of the former USSR.
- Vibe-Petersen, S.**, Leirs, H. and van Gulck, T. Predation pressure and population dynamics in African *Mastomys* rats: possibilities for integrated pest management?
- Wang, M.J.**, Zhong, W.Q., Wan, X.R. and Wang, G.H. Seasonal reproductive patterns of the Mongolian gerbil in Inner Mongolia, China.
- Wang, S.Q.**, Yang, H.F., Hao, S.S. and Zhang, Z.B. Competition between the rat-like hamster and the striped hamster.
- Wang, Y.**, Guo, C., Zhang, M.W., Li, B. and Chen, A.G. Population fluctuation of *Microtus fortis* in Dongting Lake area, Hunan, China.
- Cowan, D.P., Bull, D.S., **Watkins, R.W.** and Smith, P. A stochastic model of the responses of farm populations of the Norway rat to anticoagulant use.
- Wu, D.L.** Population fluctuation of a rodent pest in Yunnan, China.
- Yang, H.F.**, Wang, S.Q., Hao, S.S., Zhang, Z.B., Yang, W.P., Cao, X.P. and Wang, F.S. Reproductive characteristics, growth and development of the rat-like hamsters (*Cricetulus triton*).
- Zhou, H.**, Qi, G.Z., Zhou, X.P., Li, Z.Q. and Chen, Y.N. Survey of rodents living around Beijing Capital airport.

Symposium B: Rodent physiology and adaptation of rodents

Oral presentations

- Hume, I.D.** Dietary and digestive adaptation of rodents.
- Wang, D.H.**, Wang, Z.W. and Wang, Y.S. Energetics and thermoregulation of small mammals on the Qinghai–Tibet plateau.
- Liu, X.T., **Li, Q.F.**, Lin, Q.S. and Sun, R.Y. Variations in mitochondrial thermogenesis and expression of an uncoupling protein gene in brown adipose tissue from Mongolian gerbils during cold exposure.

Poster presentations

- Bao, W.D.**, Wang, D.H., Wang, Y.S. and Wang, Z.W. Seasonal changes of non-shivering thermogenesis in small mammals from an inland semi-arid region on the Ordos Plateau, Inner Mongolia.
- Bao, W.D.**, Wang, D.H., Wang, Y.S. and Wang, Z.W. Seasonal variation in the digestive tract morphology of four species of rodent in the Ordos semi-arid region, Inner Mongolia.
- Bao, W.D.**, Wang, D.H., Wang, Y.S. and Wang, Z.W. Energy metabolism and thermoregulation in the desert hamster (*Phodopus roborovskii*) in the Ordos semi-arid region, Inner Mongolia.
- Wang, D.H.**, Wang, Y.S. and Wang, Z.W. Metabolism and thermoregulation in the Mongolian gerbil *Meriones unguiculatus*.
- Wang, D.H.** and Wang, Z.W. Metabolism and thermoregulation in root voles (*Microtus oeconomus*) on the Qinghai-Tibet plateau.
- Wang, Y.S.**, Wang, D.H. and Wang, Z.W. Maximum metabolic rate of root vole and plateau pika from Qinghai-Tibet Plateau.
- Wang, Y.S.**, Wang, D.H. and Wang, Z.W. Trade-off between reproduction and litter size in root voles.
- Wang, Y.S.**, Wang, D.H. and Wang, Z.W. Effect of photoperiod and temperature on metabolic rates in Plateau pika and root voles.

Symposium C: Control techniques (biological control, habitat management, ecologically based management etc.)

Plenary lecture

- Grant Singleton** (Australia), Rodent pest management in Southeast Asia—an ecological approach.

Oral presentations

- Hinds, L.A.**, Lawson, M.A., Jackson, R.J. and Shellam, G.R. Development of fertility control through viral or oral delivery of immunocontraceptive agents: relevance for rodent management.
- Chambers, L.**, Singleton, G.R. and Hinds, L.A. Viral-vectored immunocontraception as a potential control strategy for house mice in Australia.
- Colvin, B.A.** and Jackson, W.B. Urban rodent control programs for the 21st century.
- Murakami, O.** and Tristiani, H. The integrated management of the rice field rat (*Rattus argentiventer*) in West Java.
- Leung, L.** and Sudarmaji Population ecology of the rice field rat, *Rattus argentiventer*: implications for management.
- Campbell, E.** Current trends in rodent damage management for Hawaiian agriculture and conservation.
- Brown, P.R.**, Hung, N.Q. Hung, N.M. and van Wensveen, M. Rodent management in Vietnam.
- Boonsong, P.** and Hamarit, G. Preliminary study assessing integrated rodent management strategies for soybean crops in Thailand.
- Fan, N.C.**, Zhou, W.Y. Wei, W.H. and Wang, Q.Y. Rodent management in Qinghai-Tibet alpine meadow ecosystem.

- Zhong, W.Q., Wang, M.J., and Wan, X.R. Ecological management of Brandt's vole in Inner Mongolian grassland, China.
- Zhong, W.Q., Wang, M.J. and Wan, X.R. Ecological management of voles (*Microtus brandtii*) and pikas (*Ochotona daurica*) in Inner Mongolian grasslands.
- Leirs, H. Ecologically based rodent management in Africa: no quick solution for urgent problems.
- Sicard, B. Chronobiology applied to rodent pest management—the case of semi-arid agriculture in sub-Saharan West Africa.
- Shchipanov, N.A. Rodent pest control in relation to population organisation.
- Yabe, T. Bark-stripping of tankan orange, *Citrus tankan*, by the roof rat, *Rattus rattus*.
- Makundi, R.H. Towards an ecological approach for management of plague reservoirs and vectors in the western Usambara Mountains in Tanzania, East Africa.
- Stuyck, J., Berwaert, K. and van Gulck, T. A promising new approach in muskrat control (*Ondatra zibethicus*): the introduction of eradication standards.
- Khoprasert, Y., Jaekel, T., Hongnark, S. and Suasa-ard, K. Use of *Sarcocystis singaporensis* as a biocontrol agent against the Malayan wood rat, *Rattus tiomennicus* in oil palm plantations in Thailand.

Poster presentations

- Dou, Q., Li, F. and Mai, T. Ecological and socio-economic factors influencing integrated rodent management (IRM) in rural areas of Yunnan, China.
- Douang-Boupha, B., Schiller, J.M. and Bounnaphol, O. Rodents in agriculture in the Lao PDR.
- Huang, X.Q., Feng, Z.Y., Shuai, Y.Y. and Yuan, S.X. Ecological characteristics and integrated management techniques for *Rattus rattoides*.
- Li, J.H., Yue, M.S. and Liu, Q.Y. A field trial of integrated management of commensal rodents in the residential quarters of the urban area.
- Liao, L.F., Zhong, Y.S., Zhang, L.S., Jiang, X.Y., Yu, X., Jiang W. and Li W. The pest characteristics and control of rodents in Tulufan agricultural area.
- Rahmini and Sudarmaji, Age structure and breeding performance of the rice field rat in West Java.
- Singleton, G.R., Brown, P., Mills, A. and Lewis, A. Rodent management and support network in Southeast Asia.
- Sudarmaji, Jumanta and Rochman. Rice as a trap crop using trap barrier system for controlling the rice field rat (*Rattus argentiventer*) in West Java, Indonesia.
- Thuyet, L.V., Singleton, G.R., Tuat, N.V., Tan, T.Q., van Wensveen M. and Tuan, N.P. Management of rodent pests in the Red River delta, Vietnam.
- Wu, X.D. and Fu, H.P. The primary application of classification of types of rodent damage for regional rodent control.

Symposium D: Control techniques (chemical control and resistance; physical control etc.)

Plenary lecture

Dale Nolte (United States of America), Current status of rodent management in the United States.

Oral presentations

Buckle, A.P. The management of rodent pests of agriculture—20 years on from the Paris OECD/FAO/WHO Expert Consultation.

Pelz, H.J. and Endepols, S. Development and field evaluation of a blood clotting response resistance test with rats using coumatetralyl.

Prescott, C.V. and Buckle, A.P. Resistance test methodologies—a novel test procedure for the potent second generation anticoagulants.

Lam, Y.M. Warfarin resistance in the rice field rat, *Rattus argentiventer*.

Nolte, D.L. Impact of rodents on reforestation in the United States: Problems and management.

Sutherland, O.R.W. and Eason, C.T. Secondary poisoning risks associated with broad-scale field use of Brodifacoum in New Zealand.

Weile, P. Rat control: legislation and administration in Denmark.

Watkins, R.W., Quy, R.J., Gurney, J.E. and Cowan, D.P. Cinnamamide: a repellent for commensal and field rodents?

Dong, T.Y. Studies on resistance to anticoagulant rodenticides in China.

Liu, Q.Y., Wang, C.X. and Ma, J. Field trials with the anticoagulant 'Stratagem' against rodents in special environments.

Poster presentations

Brown, P.R., Jones, D.A. and Singleton, G.R. Management of mouse plagues in Australia using ecologically based pest management.

Burkart, S.E. Efficacy and value of Flocoumafen (STORM®), a second generation anti-coagulant rodenticides, in public health and agricultural rodent pest control.

Larsen, K.S. Leirs, H. and Lodal, J. Palatability and toxicity tests with a systemic insecticide in a rodenticide bait for rat and flea control.

Ma, Z.X., Zhang, Z.H., Chang, W.X., Liu, Z., Yan, Y.P., Guo, T.R. and Zhang, R.L. Control of rodents to alleviate poverty in the Loess plateau of China.

Moctar, K., Diarra, W., Papillon, Y. and **Sicard, B.** Effectiveness of Diphacinone and Silmine G on *Arvicanthis niloticus*.

Mwanjabe, P.S. Location of food sources in *Mastomys natalensis* Muridae, Rodentia.

Petrova, E.V., Parfenova, V.M., **Vasilieva, N.Y.** and **Apfelbach, R.** Species discrimination in interspecific hybrids of two dwarf hamster species supports the odour image hypothesis.

Sadio, T., Keita, M., Papillon, Y. and **Sicard, B.** Impact of rodents versus insects on food products stored in Mossi (Burkina Faso) and Bambara (Mali) regions.

Suasa-ard, K., Hongnark, S., Khoprasert, Y. and Boonsong, P. Rodent management in rice fields of Thailand.

Wang, T.L., Ning, Z.D., Zou, B., Chang, W.Y. and Wang, K.G. Studies of integrated rodent control in the broken Loess plateau gully region.

- Zhang L.S.** An introduction to the anticoagulant rodenticide, diphacinone sodium salt.
- Zhu, E.L., Li, P. and Wang, F.L.** The rodent problem in farming areas and progress in its control in China.
- Zhu, L.B., Ma, Q. and Zhu, H.** Integrated rodent control measures in demolition areas in the city of Shanghai.

Symposium E: Rodent chemical communication

Plenary lecture

Richard Brown (Canada), The olfactory world of the rodent.

Oral presentations

- Zhang, J.X., Wang, Z.W. and Zhang, Z.B.** Roles of gonadal hormones in the control of flank glands of ratlike hamsters (*Cricetulus triton*).
- Wysocki, C.J., Wysocki, L.M., Lepri, J.J. and Tubbiola, M.L.** Influence of the vomeronasal organ on reproduction: chemosensory cues as potential regulators.
- Johnston, R.E.** Odours, scent over-marking and mate preference.
- Vasilieva, N.Y.** The role of conspecific and heterospecific chemical cues in population dynamics—an experimental approach.
- Rozenfeld, F.M., De Jaegere, F. and Dobby, A.** Social environment in relation with the reproductive success of females in two vole species.
- Voznessenskaya, V.V.** The role of predator cues in reproduction of Norway rats.
- Heise, S., Rozenfeld, F.M. and Van Acker, A.** Hierarchical structures, regulation of reproduction, odour preferences and susceptibility to diseases in groups of female common voles, *Microtus arvalis*.
- Zhang, L., Fang, J.M. and Sun, R.Y.** Olfactory communication in Brandt's vole: individual odour discrimination in mate choice.
- Apfelbach, R. and Kruer, S.** Olfactory and cognitive abilities in senile Wistar rats.

Poster presentations

- Vasilieva, N.Y., Cherepanova, E.V., Apfelbach, R. and von Holst, D.** Influence of cat's urinary chemosignals on maturation, testosterone level and meiosis in male Campbell's hamsters (*Phodopus campbelli*).
- Voznessenskaya, V.V. and Wysocki, C.J.** Plasticity of rodent chemical communication.
- Zhang, J.X., Zhang, Z.B. and Wang, Z.W.** Sexual difference and seasonal changes in size of flank glands of rat-like hamsters (*Cricetulus triton*).

Symposium F: Rodent behaviour and implication in management

Plenary lecture

David Macdonald (United Kingdom), Berdoy, M. and Mathews, F. The brown rat: Explorations of opportunism.

Oral presentations

- Baxter, R.M., Ntshebe, B., Matshili, J. and Kelly, E.** Bark consumption by South African rodents and its implication for commercial pine forestry.

- Minato, S.**, Minato, T., Wakabayashi, M. and Hidaka, T. Arboreal behaviour of the Japanese dormouse (*Glirulus japonicus*).
- Zhou, W.Y.**, Wei, W.H. and Fan, N.C. A method for studying behaviour of small animals.
- Zhang, D.C.** and Fan, N.C. A comparative analysis of behavior between two sympatric species, *Ochotona daurica* and *C. curoniae*.
- Shi, D.Z.**, Hai, S.Z., Zhang, S.Y. and Zhang, Z.R. Studies of the social behaviour in colonies of Brandt's vole (*Microtus brandtii*).
- Wei, W.H.**, Fan, N.C., Zhou, W.Y., Yang, S.M. and Cao, Y.F. Studies of aggressive behavior of plateau pikas in the reproductive period.
- Zhao, Y.J.**, Fang, J.M. and Sun, R.Y. Familiarity and mate choice of female and male root voles, *Microtus oeconomus*.

Poster presentations

- German, A.** Incest-avoiding behaviour of Levant's vole (*Microtus guentheri*) in captivity.
- Dou, F.M.**, Li, J.H. and Yang, X.R. A battery operated animal activity recording system with a single-chip micro-computer programmed in basic language.
- Wan, X.R.**, Wang, M.J., Zhong, W.Q. and Wang, G.H. The social structure and mating system of Brandt's vole (*Microtus brandtii*).
- Yu, X.D.** and Fang, J.M. The effect of kinship on social behavior of Brandt's voles (*Microtus brandtii*).
- Zhang, J.X.**, Zhang, Z.B. and Wang, Z.W. Seasonal differences in social behavior among adult rat-like hamsters (*Cricetulus triton*).

Symposium G: Epidemiology of rodent diseases and their impact on rodent population and humans

Plenary lecture

- James Mills** (United States of America), The role of rodents in emerging human disease: Examples from the hantaviruses and arenaviruses.

Oral presentations

- Ellis, B.**, Regnery, R., Beati, L., Marston, E. and Childs, J.E. Rodent-borne *Bartonella*: their importance to human health.
- Machang'u, R.S.**, Kilonzo, B.S. and Makundi, R.H. Studies on rodent transmitted diseases in Tanzania.
- Sheikh-Omar, A.R., Lai, K.Y., Ng, B.K., **Mohad-Azmi, M.L.**, Smith, A.L., van Wensveen, M. and Lam, Y.M. A serological study for rat cytomegalovirus in rice field rats (*Rattus argentiventer*).
- Mohd-Azmi, M.L.**, Lai, K.Y. and Sheikh-Omar, A.R. Characterisation of new rat cytomegaloviruses isolated from rice field rats (*Rattus argentiventer*).
- Neronov, V.M.**, Strelkova, M.V. and Lushchekina, A.A. Interrelationship of *Leishmania* parasites and rodents in arid regions of Asia.
- Wang, C.X., **Li, J.H.**, and Liu, Q.Y. Rodent-borne diseases and their control in China.

Poster presentations

Quy, R.J., **Watkins, R.W.**, Cowan, D.P., Haynes, P.J., Sturdee, A., Chalmers, R.M., Bull, S.A. and Bodley-Tickell, A. Norway rats, reservoir hosts for *Cryptosporidium parvum*.

Symposium H: Rodents as indicators of environmental change and their role in maintenance of ecosystem

Plenary lecture

Chris Dickman (Australia), Rodent ecosystem relationships: a review.

Oral presentations

Gliwicz, J. Rodents in disturbed forest habitats.

Ieradi, L.A. and **Cristaldi, M.** Rodents as monitors of environmental contamination.

Zhang, Z.B., **Hao, S.S.**, **Wang, F.S.**, **Wang, S.Q.** and **Meng, Z.B.** The impact of rodents on forest regeneration in the mountain areas of Beijing, China.

Poster presentations

Cao V.S. The rodent diversity in Vietnam.

Dai, K., **Yao, J.** and **Hu, D.F.** Microhabitat preferences of desert rodents in the southern Dzungaria basin.

Hu, D.F. and **Sheng, H.L.** Mechanisms of coexistence of desert rodent communities in the southern fringe of Dzungaria Basin.

Ning, Z.D., **Wang, T.L.**, **Zou, B.**, **Chang, W.Y.**, **Wang, K.G.** and **Ji, J.M.** The rodent fauna composition, distribution and degree of damage in the Gully region of the Loess plateau.

Zou, B., **Ning, Z.D.**, **Wang, T.L.**, **Chang, W.Y.** and **Wang, K.G.** Natural enemies of rodents and their protection and utilisation in the Loess plateau of West Shanxi, China.

Yao, J., **Dai, K.**, and **Hu, D.F.** Microhabitat use of *Salpingotus crassicauda* in southern Dzungaria Basin.

Special interest groups/workshop

1. Rodent damage management. Chair: **D.L Nolte**
2. Resistance to rodenticides. Chairs: **A.P. Buckle** and **C.V. Prescott**
3. Asian rice field rat management. Chairs: **K.L. Heong** and **G.R. Singleton**
4. Rodent chemical communication. Chair: **N.Y. Vasilieva**

Abstracts

Symposium A

Population Dynamics—Including Forecasting and Managing Rodents

INVITED LECTURE

Current paradigms of rodent population dynamics—what are we missing?

Charles J. Krebs

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Rodent population studies have played a key role in developing our understanding of population dynamics in general and in providing a testing ground for many hypotheses about population processes. It is both a blessing and a curse that rodents are often abundant, inexpensive to investigate, and operate on a spatial scale that humans can study. The proximal stimulus to understanding rodent population dynamics is to alleviate problems of rodent pests in agriculture and disease transmission to humans. Conservation problems do not loom large in the literature on rodents.

Ideas about rodent population dynamics have gone through three phases. In the 1930s there were almost no quantitative data and population control was believed to be caused by biotic agents that operated in a density-dependent manner. By the 1950s a new paradigm of social control of numbers emerged with emphasis on physiological stress and social aggression within populations. By the 1970s a synthesis of sorts had emerged, suggesting that multiple factors caused population changes. The addition of experimental manipulation of field populations in the 1960s enlarged our outlook on the complexities of rodent populations, and the emergence of mathematical modeling and rigorous statistical analyses of survival and reproduction in the 1980s and 1990s has shown again that rodents have been the *Drosophila* of population ecology. But as precision has increased over time, generality and simplicity have declined to near extinction, and we need to reverse these trends.

What is missing and what do we need to do in the next 20 years? While we have some good short-term, experimental studies of rodent populations, we have too few long-term experimental studies. Experimentation is the key to understanding, and no study should be undertaken without a clear set of experimental predictions. The era of alpha-level descriptive population studies should be over. Second, we need large scale, extensive studies coupled with these short-term experimental studies. Rodents are good candidates for studies of spatial dynamics, a strongly emerging subdiscipline in ecology. Third, rodent management should focus on the factors limiting populations and use an experimental approach. The era of pest eradication via killing should be over and we need to be more clever in developing our management

options. The development of genetic resistance to anticoagulants and chemical poisons is a call to the ecologists of the 21st century to think more clearly about why rodent pests exist and how we might outwit them. The male penchant for killing pests should give way to the female penchant for thinking before taking the easy way in pest control. The accumulated knowledge of the physiology, behaviour, and genetics of rodents needs to be integrated into our management options. There is much to be done both to understand and to outwit these clever mammals.

PLENARY LECTURE

Rodents in China—population dynamics and management

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Rodent pests are a serious problem for agricultural production in China. Over recent decades, with changes in climate patterns, heavier droughts and warmer winters, rodents are becoming more abundant. In the early 1980s, there were broad-scale outbreaks of rodents in agricultural areas in China; 24.9% of arable land and 14% of grasslands were infested annually. Since 1986, rodent management has been a key project in the national five-year-plan. The biology and management of 15 major rodent pests from six major ecosystems have been extensively studied for more than 13 years. The key project aims to collect long-term population data for major rodents, to establish short-term (3–6 months) or long-term (>6 months) forecasting models, to understand population recovery and community succession after large-scale management, to develop effective control techniques and strategies, to establish demonstration areas and to help local government to launch a large-scale rodent control campaign. The population dynamics and management strategies vary greatly and depend upon the species and its ecosystem.

In the Northern Plateau with dry farmland, the rat-like hamster (*Cricetulus triton*) and striped hamster (*C. barabensis*) are dominant species. The striped field mouse (*Apodemus agrarius*) becomes dominant in some wet areas with good irrigation. The former two hamster species showed a similar pattern of outbreaks in 1982, 1986 and 1993, and these corresponded with El Niño episodes. After ditch-irrigation was changed to a spray irrigation system, the rat-like hamster was observed to outbreak in some areas of Beijing where previously the striped field mouse was dominant. The sterilising effects of alpha-chlorohydrin have been tested effectively in the laboratory on the rat-like hamster. A multiple-capture trap with magnetic trigger was invented for catching the rat-like hamster.

In the Northwest Loess Plateau with very dry croplands, Chinese zokor (*Myospalax chinensis*), an underground dwelling rodent, and brown voles (*Microtus spp*) are major rodent species. The populations of Chinese zokors are stable. This species seldom comes above ground, and is also very cautious of rodent baits, making traditional

direct baiting ineffective. Tube-bombs with firework material have been successfully developed for controlling zokors in this region. Ecological management including use of herbicides, reducing waste land and flattening the farmland were effective in reducing damage by zokors.

In the steppe grassland of Inner Mongolia, the two major rodent pests are Brandt's vole (*M. brandti*) and Mongolian gerbil (*Meriones unguiculatus*). Both species show irregular outbreaks every 3–5 years. Mongolian gerbils occurred mostly in the mixed areas of grassland and cropland. Over-grazing by cattle and cultivation are key factors allowing infestation by voles and gerbils. Ecological management measures, such as controlling over-grazing by setting the date of spring-grazing 10–15 days later than usual, were found to be effective.

In the Qinghai–Tibet alpine meadow ecosystem, plateau zokor (*M. baileyi*) and plateau pika (*Ochotona curzoniae*) are major pests. The population of plateau zokors, the underground species, is stable while the population of plateau pika shows irregular outbreaks. Heavy snow is difficult for pika populations but it facilitates survival of zokors in winter. Direct baiting works well for controlling pika but not zokor. A baiting machine, which puts baits in a simulated burrow system that crosses the tunnels of plateau zokor, was invented, and the efficiency of control has greatly increased. A botulin-toxin-C was found to be very effective in controlling zokors and pikas in this region. As in the steppe grassland of Inner Mongolia, over-grazing and cultivation are key factors for increasing rodent infestation. Therefore ecological management measures including over-grazing control, and planting herbs in the degenerated rangelands after chemical control are also important for sustainable integrated management.

In the rice-field region along the Yangtze River, Norway rats (*R. norvegicus*), striped field mouse (*Apodemus agrarius*) and *R. nitidus* are major pests. The population of rats is stable between years. Striped field mouse was negatively affected by heavy rain and flooding. Oriental voles (*M. fortis*) are the major pest near Dongting Lake and their reproduction and migration are affected by heavy flooding. They inhabit the beach area of Dongting Lake in the non-flooding seasons but migrate to rice-fields around the lake during the flooding season and cause serious crop damage. Blocking the migration path of voles between the rice-fields and the lake beach using a barrier system along the beach dam was very successful in reducing the huge crop damage.

In the rice-field of the Pearl River Delta, *R. losea* and *Bandicota indica* are major pests. The numbers of both species are stable between years. Baiting with rodenticides in different seasons achieved different efficiencies of control. The population of *R. losea* recovered quickly, within 3–6 months after baiting with rodenticide. *B. indica* is very cautious of physical traps and is becoming more abundant in this region due to development of industry that has changed cropland into a mosaic of waste lands.

The future studies of the national key rodent project will focus on: (1) population dynamics to understand the population outbreaks and to set up long-term forecasting models; (2) behaviour and chemical communication studies to develop effective baiting

techniques; (3) development of sustainable control techniques including fertility control and habitat management; and (4) improvement of existing anticouagulants and determination of the potential of natural and biological materials for controlling rodents.

ORAL PRESENTATIONS

Populations of African rodents: models and the real world

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Most field rodent pests display irregular population outbreaks during which damage to standing crops is devastating. Therefore, there has been a wish to be able to predict such outbreaks for several decades. The earliest models were based on observed correlations between outbreaks and preceding abnormal events such as unusual rainfall. At a later stage, theoretical deterministic population dynamics models were used and, more recently, models containing some degree of stochasticity and parameterised with data obtained from long-term biological studies were proposed.

The last-mentioned models combine a theoretical concept of population dynamics with empirical information. Therefore, they are useful both to better understand population dynamics as well as to simulate what happens in the real world. The first objective is reached even if the model performs very poorly, because that would at least document the gaps in our knowledge. However, the model's practical use is highly dependent on its accuracy. Poor performance in practical simulations may lead to wrong predictions about future population development or the potentialities of new management approaches.

This is illustrated with models that were constructed for populations of *Mastomys natalensis* rats in Tanzania. Using independent data sets, the robustness of the population models is tested and their sensitivity to stochasticity or poor parameter estimation is evaluated. Suggestions for improving the existing models and the interpretation of the simulation results will be presented.

Seasonality and population cycles in small rodents

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Referring to *Clethrionomys rufocanus* in Hokkaido and in northern Finland, the seasonal component of population regulation is discussed. Based on empirical information, it is demonstrated that the degree of density-dependence is stronger during the winter than the summer. It is furthermore shown that a major cause of the observed population fluctuations may be due to this seasonal forcing. It is furthermore demon-

strated that observed non-linearities (or phase-dependencies) may primarily be due to the density-dependent structure during the winter.

The Finnish data used cover a period of 49 years, whereas the Hokkaidian data consist of 225 time series mostly covering between 20 and 30 years; in the presentation, analyses based on these two sets of data are summarised. As part of the presentation two sets of mathematical models are presented and discussed—one based on statistical time series modeling and the other based on assumptions common within the field of ecological modeling.

The influence of high temperature and migration on reproduction of *Microtus fortis calamorum* in the Dongting Lake area

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From early autumn to spring *Microtus fortis* live on the beach of Dongting Lake when the water level of the lake is low. As the water level rises in spring or in early summer, the area of the lake beach is narrowed, and *M. fortis* migrate across the dike into the farmland. When the lake beach re-emerges in autumn, the voles return. After 3 years of field investigations and laboratory observations, we have determined that the high temperature in summer and migration are two key factors influencing on the reproduction of *M. fortis*.

Most microtine rodents occurring at high latitudes (above 35°N) breed mainly in summer. However, in the Dongting Lake area (28°13' 29°55'N, 111°11–113°43'E), *M. fortis* show a different pattern of reproduction. They breed all year and the average pregnancy rate of adult females is 37.1%, although the pregnancy rate is very low in summer (June–August). In 1992, no pregnant voles were captured in summer, while in 1993 and 1994, the pregnancy rates were 15.9% and 4.5%, respectively. The pregnancy rates in winter were high, 72.3% in 1992, 50.0% in 1993 and 66.7% in 1994. The reproductive dynamics of males were similar to that of females, with some males showing small testes in the summer. In 1997, a laboratory experiment was conducted to test whether the high temperature in the summer affected the breeding potential. Voles captured on the beach were paired ($n = 53$ pairs) and held under natural temperature and light/dark cycle in summer (June–August) or under artificial conditions (21–23°C, 12L:12D). There was no significant difference in pregnancy rates in June and August, but in July, pregnancy rates under artificial conditions were significantly greater than under natural conditions.

In the farmland the lowest breeding rate of *M. fortis* occurred in June which was not the hottest month. Generally, migration occurred in May and the testes of the males became small in June, one month after the migration. We think this response was related to the stress of the migration during flooding. In 1992 the flood season began earlier than usual, in March. Although *M. fortis* were forced to migrate into farmland, the breeding rate of both sexes in April was still high. In 1994, some voles moved

into farmland after heavy rain in April, and also had high breeding rates. Why did both sexes retain high breeding potential after migration in March? We conclude it is because temperatures in April are still suitable for breeding. So the high summer temperature was the main factor influencing reproduction in *M. fortis*, and the stress of migration forced by the flood enhanced this effect.

Reconsideration of lemming phylogenetic history with special reference to the origin of *Synaptomys*

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True lemmings (Lemminae) at present are the most common rodents that inhabit the Arctic tundra of both Old and New World and are very well known for periodic rapid increase of population densities, sometimes followed by migrations. At the same time, despite the rather good representation in Late Caenozoic sites, the early history of the group and phylogenetic relations of the genera are confused. In order to clarify the phylogenetic and taxonomic relationships of a number of forms described from Pliocene and early Pleistocene in Eurasia and North America, comparative analyses of vast fossil lemmings material from Late Caenozoic sites in Poland, Western and Eastern Siberia and other regions have been performed. All characters used in phylogenetic analysis and taxonomic interpretations earlier were considered and revised; new ones also have been included. Analysis of variation of masticatory surface patterns in M3 (character of greatest importance in taxonomy and systematics of Lemminae) from Late Vilanyian site Zamkova Dolna Cave (Poland) clearly shows that remains earlier referred to *Synaptomys* in Eurasia actually belong to *Lemmus*. In this sample a full range of variation (total number of teeth = 87) can be observed: from teeth corresponding in the masticatory surface pattern to *Synaptomys* (*Plioctomys*), 14% to recent *Lemmus* (also 14%), with all possible transitions among these extremes. The morphology of other teeth in this sample where the significant difference between the two genera is marked (M2, M1, the structure of the lower jaw), meanwhile, it is typical of *Lemmus* structure, so there is no doubt that this sample should be referred to the *Lemmus*. From the other side, comparison of teeth with the most primitive among this sample (*Synaptomys*-like) tooth structure with the teeth described from sites of older geological age as *Synaptomys europaeus* (Rebelice Krolewskie, Poland) and *Synaptomys mimomiformis* (Simbugino, South Ural) showed that there is no major difference in their morphology and no doubt that these teeth belong to one evolutionary line and, hence, should be referred to the *Lemmus*. This conclusion essentially changes the generally accepted viewpoint on the history and phylogenetic relationships of the genera of Lemminae. It means firstly, that the oldest remains of the group belong to the genus *Lemmus*, and, thus, it is the most ancient and primitive genus in the group. Secondly, there were no remains and no evidence of any occurrence of bog lemmings in Eurasia and the origin and evolution of the latter is therefore exclusively connected with North America. Two hypotheses of phylogenetic relationships can be formulated and tested further. According to the first one, true and bog lemmings are the sister groups, whose split occurred in the

Late Pliocene of North America, after the first migration of true lemmings (*Lemmus*) which possibly took place around 3 million years B.P. Under the other one, bog lemmings of North America are an independent line of evolution that developed in parallel, with similar teeth morphology, from different cricetid ancestors in response to the requirements of the similar food niche. Comparative analyses of the structure of lower jaw and palate of first representatives of *Svnaptomys* species of North America and first species of *Lemmus* in Eurasia are needed to test these hypotheses.

Specific features of the distribution of the great gerbil (*Rhombomys opimus*) in central Asia

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Studies of the great gerbil's range and distribution in Central Asia were analysed from published data, museum collections, natural maps and the authors' field observations. A preliminary scheme was plotted for range regionalisation, in which three parts have been isolated or, according to a 1971 classification of Dubrovskii and Kucheruk, three regional complexes of autonomous groups of populations are distinguished: Dzungarian, Central-Gobi (or Beishan) and East-Gobi-Alashan. Five autonomous population groups have also been isolated which are to the north of the main range: Shargin-Gobi, Beger-nuur, Orok-nuur, Bulgan and Bayan-Dov. West of the main area of the great gerbil distribution, an isolated colony is in the Ili river valley, connected with the Kazakhstan portion of the range (Ili regional complex of autonomous groups of populations). Regions with favourable conditions for great gerbil colonies were also shown. Additional field observations are required for more detailed description of the great gerbil range.

The diet and dynamics of New Zealand's forest-dwelling house mouse (*Mus musculus*) in the Orongorongo Valley

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Monitoring of house mice living in the mixed beech (*Nothofagus* spp.) and podocarp/hardwood forest of the Orongorongo Valley, New Zealand began 1971 with a view of examining the relationship between mouse numbers and intermittent production of beech seed. Over the 104 quarterly-trapping sessions, mouse catch rates ranged from 0 to 13.7 mice per 100 trap nights. The initial hypothesis that mouse numbers in the forest fluctuate in relation to food (beech masting and arthropod abundance) prompted us to examine the arthropod diet and breeding of mice between 1992 and 1996.

Overall 85% of the 254 stomachs examined contained some form of arthropod. Sixty-eight percent of mice had eaten spiders, 52% had eaten caterpillars, and 47% had eaten other taxa such as beetles, centipedes, amphipods, and fly larvae. Spiders

were eaten consistently throughout the year while the consumption of caterpillars varied seasonally. The consumption of beetles and other taxa was sporadic. The most commonly identified prey were the spider *Miturga* sp. and the tortricid caterpillar *Cryptasasma querula*.

Mice caught at beech trap sites ate different arthropods to those caught at podocarp/hardwood trap sites. *Cryptasasma querula* was most often eaten by mice caught at podocarp/hardwood trap sites while another caterpillar group *Tingena* spp. was most often eaten by mice caught at beech trap sites. Mice living in beech ate more beetles than those caught in podocarp/hardwood. Differences in food eaten were also reflected in differences in trap catch and body weights of mice. Mice caught in stands of podocarp/hardwood weighed 6% more than those caught in stands of beech and mice were always caught in stands of podocarp/hardwood while they were rarely caught for 18 months at beech trap sites. Our findings suggest that, in the Orongorongo Valley, stands of podocarp/hardwood may act as mouse donor habitat while beech is acting as mouse reception habitat. Analysis of changes in mouse catch rates since 1971 suggest that population fluctuations in both habitats are density dependent and closely related to beech seed fall. We can now predict with reasonable accuracy the timing of peaks in mouse numbers in beech habitat.

The cohort life table of the Brandt's vole (*Microtus brandti*) in Inner Mongolian grasslands, China

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This work was carried out in the typical steppe of the Inner Mongolian grassland in North China from 1995 to 1996. The life data of 320 voles, *Microtus brandti*, were obtained by capture-recapture techniques and by direct observations in two field populations, a wild population (43°25', 116°41') and an enclosed population (43°37', 116°41'). The procedure, Survival Analysis, of the shareware package, STATISTICA Release 4.5A, was used for data analysis.

Our data have indicated that many deaths occur in the early life stage of the Brandt's vole. The median life is about 50% shorter than that of expected life of the same cohort. The characteristics of the survivorship curves of this species suggest a lower survival rate in the early and later life stages with a higher survival rate in the middle life stage, producing an n-shaped survival curve. The type of survivorship curve of this species is B or between types B and A. The ecological longevity of *Microtus brandti* is about 18 months.

There is no significant difference between sexes in this species. Differences in survival of each sex are often thought to be due to the species' sexual selection and mating system. In polygynous species, males generally have lower survivorship than females during most stages in life, and a shorter lifespan. On the contrary, in many monogamous species, males have a similar or higher survival rate than females.

However, in our studies, Brandt's vole exhibited no differences between the sexes despite its polygynous mating system. One explanation is the delay in maturation of new born males which may reduce the injury caused by the intrasexual competition and combat. As a result, the mortality rate of these sub-adult males may be reduced.

Offspring of females which over-winter have a higher survival rate than offspring of current season females. This could be due to the maternal behaviour of over-winter females which are in better physical condition and more experienced breeders than younger females born in the current season. Another explanation may contribute to inbreeding. Previous work has shown that families of Brandt's voles re-form in the early spring with all over-winter males dispersing from their original groups, while most of the females remain. As a result, over-winter males are not closely related to over-winter females in the same group and offspring are not inbred. However, in the following breeding season, most of the voles including the adult newborn females seldom move from their original group. Therefore, father-daughter matings occur and offspring have a lower survival rate than offspring of over-winter females.

Rodent population dynamics under environmental change: is it an ergodic process?

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Rodents are assumed to respond to environmental change by altering population numbers and distribution in accordance with species-typical ecological demands. When analysed in space, variation in population and community structure appears to be closely associated with varying conditions. Rules operating at spatial scale are often implied for analyses and forecasts of the population dynamics in a changing environment. This is done at a temporal scale proceeding from the assumption of its ergodicity. Here we present data on the long-term (1980–1997) dynamics of the rodent community in the semi-deserts of southern Russia (Republic of Kalmykia) under the conditions of rapid recovering succession, induced by recent dramatic reduction of live-stock pasturing and a new cycle of climate humidisation. Desert with low sparse ephemeral cover changed in the early to mid 1990s to steppe-like landscape covered with dense tall perennial grass. As a result we expected decrease in numbers and extent of distribution of the psammophil gerbil *Meriones meridianus* and a population increase in mesophil species *M. tamariscinus*, *Microtus socialis*, *M. rossiaemeridionalis* and *Spermophilus pygmaeus*. Species abundance and distribution were estimated in various habitats within a 20 km² area in the south of Kalmykia (Chernye Zemli) in 1980–83 and in 1993–97. The surveys were carried out along transects (50 snap-traps set in lines for 3 days) and at stationary 1 ha grids by means of capture-recapture methods (100 trap stations set in squares 10 × 10 m for 2 hours during two weeks). Species status within the community was estimated through *relative abundance* of a particular species in the total number of rodents captured. Extent of distribution was measured as the proportion of key sites inhabited by particular

species. Species abundance was estimated through *relative trappability* on snap-trap transects (ind/100 day-traps) and as *local density* within live-trap grids (ind/ha).

Population status of *M. meridianus* has not changed significantly despite the marked reduction of normally preferred open sandy-soil habitats with sparse vegetation. In both periods this species occurred everywhere at relatively high and stable numbers. *M. tamariscinus* avoided open and slightly covered sands, and was not abundant and occupied few habitats in the 1980s. In the 1990s this gerbil had dispersed widely, significantly increased in numbers and was equally dominant with *M. meridianus* in almost all types of habitats. Contrary to expectation, abundance and extent of distribution of *S. pygmaeus*, typical representative of the steppe fauna, decreased. There was some population growth only in 1997. *M. socialis* kept the status of rare species during the whole period of observations up to 1997, when population numbers increased by 20–40 times and the species spread everywhere dispersing in non-typical habitats. Unusually high snow cover, rather than vegetation succession, appeared to induce this peak. Single individuals of *M. rossiameridionalis* were recorded within the study area for the first time only in 1997. Thus, rapid recovering succession has not resulted in a marked response by the rodent community. The results in part contradict an assumption that the phases of temporal variation in species abundance and distribution under changing environment have analogues in space. In particular, both gerbil species sympatric on the large parts of their geographical ranges, show different habitat preferences in accordance with different ecological requirements and rarely occur together at high densities. Discrepancy between expected and observed species' response may indicate some kind of population "inertia", constraints being previous population state and associated social processes. Prognostic models developed on the basis of the rules operating at the spatial scale should be considered with caution since ergodicity is not likely to be an attribute of biological systems.

Models for predicting plagues of house mouse (*Mus domesticus*) in Australia

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The introduced house mouse (*Mus domesticus*) is a major pest in the grain-growing regions of southern and eastern Australia. The population dynamics of mice differs significantly between the relatively frequent outbreaks in the Darling Downs in Queensland and areas with mostly low abundance of mice and occasional eruptions to plague proportions as in the wheat-belt of New South Wales, Victoria and South Australia. The different dynamics imply that the major regulating factors are not uniform between regions.

There are at least eight models, with varying degrees of predictive ability, that describe the development of mouse plagues in Australia. They include: broad-scale regional models that rely on environmental or production data; district and small-scale models that describe in detail the processes of plague formation; and simplified

'process' models focusing on one or more mechanisms that might influence the rate of change of mouse abundance.

In this paper we describe recent modifications to a model for predicting the onset, magnitude and duration of mouse plagues in the cereal production areas of the Victorian mallee. A secondary aim is to assess the efficacy of viral- or bait-delivered immunocontraception for managing mouse plagues. The model is based on a 16-year data set that has tracked four major eruptions of mice. Separate numerical response functions for breeding and non-breeding seasons, and environmental indices for the onset and termination of breeding, were used to match computer simulations with the observed population trajectories. As well, the model was validated by using records of plagues for the last 100 years to test predictions of the frequency of eruptions. The structure of this computer simulation model is compared with other published models for similar climatic regions. Potential areas for future development will be discussed.

Analysis of the effects of predation and food availability on population dynamics of root voles

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This study determined the effects of interactions between nutrition, predation, and spacing behaviour on the population demography of root voles, *Microtus oeconomus*, using a factorial experimental design in enclosures in the field. The effect of predation and patterns of food availability on the population dynamics of the voles is described. The specific hypothesis tested is that the availability of high-quality food, and predation act independently and additively to limit the population densities of small rodents.

The results from four experimental treatments generally supported the hypothesis that food availability and predation have independent and additive effects on the vole populations. The predictions that the populations with supplementary food and no predation would reach the highest densities, that those with no supplementary food and no predator access (control) would show the lowest densities, and that those with a single treatment would have intermediate densities, were confirmed. A two-way ANOVA indicated that both food and predation treatments had significant effects on densities during weeks 1–20. Prevention of predator access significantly affected recruitment during weeks 4–20, but the effects of additional food on recruitment was less and only marginally significant.

The effects of both food and predation treatment on the densities and recruitment appeared to be additive (no significant interaction) and different in magnitude. Also as expected, the patterns of recruitment and the instantaneous rate of population increase under four different treatments paralleled the observed density patterns.

The role of food limitation in irruptions of Australian desert rodents

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Natural irruptions of desert rodents are generally characterised by sudden increases in numbers following rainfall. Australian desert rodents follow this same pattern and it has been suggested that the sudden increase in numbers is due to an increase in food. However, reports of irruptions in Australia tend to be anecdotal with little or no supporting evidence for causal factors. Here I report the results of a study investigating food limitation in populations of Australian desert rodents in relation to irruptions. The study was carried out in the Simpson Desert in southwestern Queensland and concentrated on two endemic species: *Notomys alexis* and *Pseudomys hermannsburgensis*.

In the natural situation, populations of both *P. hermannsburgensis* and *N. alexis* showed strong temporal fluctuations. For both species, numbers of individuals were correlated significantly with an index of rainfall with a time-lag of four months. Four months after large rainfall events, both species showed a peak in population numbers. Numbers of rodents increased primarily as a result of reproduction on both local and regional scales. All members of the population, apart from lactating females, appeared to be highly mobile, resulting in low residency time and a high turnover of individuals within the local population.

Pseudomys hermannsburgensis, which is largely granivorous, showed a positive relationship with seed availability both temporally and spatially. With declining availability of seeds in the sand, numbers of *P. hermannsburgensis* showed a corresponding linear decline. On a small spatial scale, numbers of *P. hermannsburgensis* captured per trap were correlated positively with the availability of seeds at each trap station. This spatial correlation suggests that *P. hermannsburgensis* can respond to spatial variation in food availability; tied in with movement patterns of individuals, it suggests that habitat selection may play a role in determining local population levels. *Notomys alexis*, which also include much seed in the diet, showed a non-significant temporal trend with seed availability, declining in numbers through the period of seed decline. There was no spatial relationship between numbers of *N. alexis* and seed availability. These data suggest strongly that rainfall and possibly rain-induced food availability trigger natural irruptions of Australian desert rodents.

A series of supplementary feeding experiments was used to directly test the hypothesis that populations of *P. hermannsburgensis* and *N. alexis* are food limited. The addition of sunflower seeds to a series of trap plots resulted in increased numbers of *P. hermannsburgensis* compared with control plots. The response of this species was quite specific in that animals responded only to food placed at the bottom of dunes. The density of *P. hermannsburgensis* was related directly to the amount of supplementary food available, and the amount of food consumed. *Notomys alexis* showed an increase in mean body mass as a result of supplementary feeding, but population

density did not change. Neither species showed a long-term response to the dispersion of supplementary food (clumped or spread). Supplementary feeding was not able to reverse a population decline, but it did slow the overall rate of the decline in *P. hermannsburgensis*. The combination of pattern analyses and experimental manipulations suggests that populations of *P. hermannsburgensis* are limited by availability of food, whereas populations of *N. alexis* are not.

Can population growth rates vary with the spatial scale at which they are measured?

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Cyclic small mammal populations often exhibit lower than maximum growth rates following their decline. This phenomenon is known as the extended low and is thought to be an important clue to the solution of the mystery of why the populations seem to have a slow population recovery after a population decline to very low numbers. We identify three simple sources of bias in the estimation of population growth rates that should be considered before more complex ecological hypotheses are proposed to explain this phenomenon. First, we show that the commonly used method of adding a constant to time series data to avoid problems caused by division by zero can lead to underestimation of growth rates at low densities. Second, we suggest that sampling variance around density estimation can lead to positive bias in the estimation of growth rates when populations are distributed in ephemeral patches. Third, we show that the use of trapping grids smaller than twice the characteristic range of natal dispersal to estimate population growth rates at low densities can lead to negatively biased estimates. We analyse data from growing populations of bank voles and snowshoe hares and show that robust positive correlations exist between estimates of growth rate and the spatial scale at which population density estimates were conducted. These observations are discussed in relation to our identified sources of bias.

Seasonal changes in the population density and reproduction of the rice field rat, *Rattus argentiventer* (Rodentia: Muridae) in West Java

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The purpose of the present study was to investigate the seasonal population abundance of the rice field rat in a two hectare experimental field by using the capture-recapture method and to find the major factors affecting the above estimated population fluctuations.

Field work was conducted from 1988 to 1990 at the Jatisari Forecasting Center in West Java, about 120 km east of Jakarta. The centre is an agricultural research station (2 ha) which has rice as its main crop. Population survey by the capture–recapture method was conducted on a 2 ha experimental field surrounded by a 40 ha area of local farmland. The rice in the experimental field was planted one month after the rice field in the neighbouring farmlands. This was done so data on rat populations in asynchronous fields could be collected. Single capture live-traps made of wire mesh were baited with whole grain. The traps were checked every morning for 5 days. Trapping was conducted twice monthly. The reproductive condition of males was estimated by examining the position of the testes. Females were classified as reproductively active if they were pregnant or lactating.

Fluctuations in the size of rat populations were clearly marked by two distinct peaks per year. The population began to increase during the seed ripening phase during the rainy season and during the milky stage during the dry season. In 1988, the highest population size was estimated to be 1529 per 2 ha; this population caused severe damage to the rice crop with almost no rice harvested. Peaks occurred 2–4 weeks after harvest, and gradually decreased for about 2 weeks during the rainy season and 3 weeks during the dry season. These peaks were caused by the recruitment of young rats and immigration. In the rainy season for both years, the mating season was from January to mid-February (the panicle premordia initiation to milky stage), and births occurred from mid-February to mid-April (ripening to post-harvest). In the dry season of 1988, the mating season was from mid-April to mid-June (panicle premordia initiation to booting), and births were from mid-June to mid-August (flowering to harvest). The dry season crop in 1989 was planted later: the mating season was from mid-April to mid-July and births were from mid-July to late-September. The breeding season declined with the disappearance of rice plants after harvest each year. Survival was generally low during the mating season and high during the birth season. Survival rate was lowest in the non-breeding season (during non-cultivation). In general, the ripening stage of the rice plant was the major nutritional factor affecting the population fluctuation.

Forecasting the relationship between population size of the striped hamster and ecological factors

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This paper applies the theory of the gray interrelation analysis to the forecast of the relationship between the population size of the striped hamster and ecological factors. We selected some systematic data that related to the striped hamster population and the related ecological factors from a 10-year database for the North China Plain. We regard the population size and related factors as the main factor array and relating factor array, respectively. By using the gray interrelation theory, we can get the following result:

$$r_{05} = 0.880796; r_{03} = 0.879127; r_{01} = 0.873885; r_{02} = 0.871899;$$

$$r_{08} = 0.838137; r_{07} = 0.834565; r_{04} = 0.833309; r_{06} = 0.540963.$$

In this paper, r_{01} , r_{02} to r_{08} stand for the relating degree between the sex ratio, pregnancy ratio, average litter, age structure [(juvenile + subadult)/(adult + old)], extremely high temperature and extremely low temperature, total precipitation, extremely high precipitation and the population size, respectively. According to this, we can divide these factors into four levels: (i) extremely high temperature, average litter number; (ii) sex ratio, pregnancy ratio; (iii) extremely high precipitation, total precipitation, age structure; (iv) extremely low temperature. It was found that the population size of the striped hamster was highly affected by the extremely high temperature and the average litter number. The theory of the gray interrelation analysis can be successfully used to forecast the population size of farmland rodents and can reflect the real state of the farmland ecosystem more closely.

POSTER PRESENTATIONS

Variation, taxonomy and distribution patterns of the genus *Lemmus* in the palaeartic

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Brown or true lemmings (*Lemmus*) are the most prolific rodents of the recent tundra. They have very wide distribution all over the Holarctic tundra zone, including islands of the Polar basin. However, despite their important role in the tundra's ecosystem the taxonomic structure, distribution patterns and character of morphological variation are insufficiently known.

There are many contradictions about the rank and number of forms comprising the genus *Lemmus*. The primary aim of the current work was to examine the interpopulation variation of skull morphology and pelage colour in 13 lemming populations across the Eurasian Arctic and to elaborate on this basis any possible taxonomic interpretations. The major part of the material for this study was gathered during the Russian–Swedish Tundra Ecology Expedition during June–July 1994 in 13 sites in the Arctic tundra from Kola Peninsula on the west to Western Chukotka on the east, including the Novosibirskie Islands (I. Kotelnyi and I. Fadeyevskiy) and Wrangel Island. A complex of linear measurements and indexes (28 in total) describing the shape, proportions and sizes of the skull and mandible were taken and processed with methods of multivariate statistics. Statistical processing of data was by ANOVA, factor analysis, cluster analysis, discriminant and canonical analysis using STATISTICA version 7.0.

With the samples analysed as a whole there is a very distinct division into two large groups: island populations and mainland populations. Most of the differences between these two main clusters are explained by the significant differences in linear sizes. Lemmings from all island populations are significantly larger than those in the mainland. All mainland populations form a very close group, but despite this closeness among the mainland populations two groups could be distinguished that conditionally

designated as west and east group. Canonical analyses have shown that despite the greater difference between the mainland and island populations, the latter group (east and west) differ in other characters which mostly reflect the proportions rather than general sizes. On the next step we excluded from the analysis the island population, considering only six mainland populations. Achalanobis distances we obtained were much smaller than in the previous case, but they are significant and typical. We can see two distinct groups along the first canonical axis, the ones we designated as east and west and each of them in its turn distinctly split on two subgroups along the axis of the second component. The boundary between west and east subdivisions lay between Eastern Taimyr and the Olenek River. The group of so-called east populations lemmings from the right shore of the Kolyma River could be distinguished on the basis of certain craniological characters. These lemmings differ karyologically from the rest of the populations studied and represent another species, *Lemmus trimicronatus*.

The same material has been used by Fedorov et al. (in press) for the study of mtDNA variation. The results obtained correspond well to the differentiation we obtained in the study of morphological variation. On the basis of synthesis of morphological, karyological and data of mtDNA variation the comprehensive taxonomical structure and probable history of distribution of the *Lemmus* are suggested.

Growth and development of the sulfur bellied rat (*Rattus niviventer sacer*)

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This study investigated the growth and development of the sulfur bellied rat (*Rattus niviventer sacer*) by raising several pregnant females in a laboratory during 1992 to 1995. Females were originally captured in the fields of Xixian in Shanxi, and were fed wheat, bean, sunflower, watermelon, fruit, insects and grasses. Observations were made daily to detect births of litters. Newborn litters were monitored for changes in body fat, size and developmental characteristics. Females giving birth produced a neonate about every 15 to 25 minutes, with the longest interval between pups being 2 hours 40 minutes.

The sex ratio (M:F) of newborns was 0.93 and the survival of newborns was high (96.3%). The average body weight of newborn females was 3.24 ± 0.12 g, and was not significantly different to the males (3.36 ± 0.91 g). Initially, body weight increased quickly with average daily growth rates of body and tail lengths (relative efficiencies of 0.9938 and 0.9970) from days 0 to 25 after birth. During this period there were no obvious differences in body weight, body length and tail length between females and males. They began to grow upper incisors at about 11 days of age, opened their eyes by about 18 days and became independent after 22 days.

This information on growth and developmental characteristics of young sulfur bellied rat could be used to understand aspects of the population ecology and control of the species.

Peculiarities of structure of dental system and morphometric variation in *Lasiopodomys mandarinus* and *L. brandti*

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At present the genus *Lasiopodomys* Lataste, 1887 is divided into two monotypic subgenera-nominative and *Lemmimicrotus* Tokuda, 1941 with the species *Lasiopodomys brandti* Radde, 1861 and *Lemmimicrotus mandarinus* Milne-Edwards, 1871. Recently in the same genus, the species *L. fuscus* Buchner, 1888 has been included that earlier was referred to the subgenus *Neodon* Hodgson, 1849. The voles of this genus inhabit the territories of Mongolia, China, Korea and Russia where the range of *L. brandti* and *L. mandarinus* is limited by the territories of Southern Transbaikal. Few studies have been conducted on the structure of the skull and morphotype variation of dental system.

One hundred and seventy specimens of *L. mandarinus*, 70 specimens of *L. brandti* and 8 specimens of *L. fuscus* from different geographical regions of Transbaikal, Mongolia and China deposited in the collections of Zoological Institute RAS, St Petersburg University and the Zoological Museum of Moscow University were examined. Twenty-four characters in the structure of the skull and dental system were involved in the analysis of seven samples of *L. brandti* populations performed using principal component analysis. Discriminant function analysis was used to distinguish subspecies forms. All three species are well identified by the interorbital ridge, sizes of auditory bullae, and proodont incisors. Within the species *L. mandarinus* two populations from Transbaikal and Mongolia belonging to one species essentially differ in the sizes of auditory bullae and proodont incisors.

Within the species *L. mandarinus* two populations from Transbaikal and Mongolia belonging to one species essentially differ in the sizes of auditory bullae, interorbital width, paraconid part of the first lower molar (E/1). Subspecies *L. b. hangaicus* Bannicov, 1948 can be identified on the combination of 7 characters with the 100% exactness. The highest morphotype variability was marked for the molars of *L. mandarinus*. The first lower molar of *L. mandarinus* is represented by 6 morphotypes with the prevalence in 84% of specimens of morphotype 5/4, 7 (in nominator; the number of salient angles on the inner part of the tooth, in denominator the number of salient angles on the outer part of the tooth, after the comma the number of closed dentine spaces). The third upper molar (M3) is represented by 9 morphotypes, the dominating ones are morphotypes 3/3, 4 (44%) and 3/2, 4 (27%). In *L. brandti* M1 is represented by five morphotypes, the morphotype 5/3, 7 is meeting more often than others (52.5% specimens). Among the seven morphotypes of M3, the dominant is the morphotype 3/3, 5 (52.5%). In both species the dominant morphotypes in the different populations of Transbaikal and Mongolia are retained. For the *L. fuscus* the three

morphotypes of M1 and M3 have been distinguished, there with the extinct voles of the genus *Allophajomys*. The third upper molar more often meets in the form of 3/3, 4 as in *L. mandarinus*, but differs by more expressed talonid. It should be that *L. fuscus* has significantly less quantity of cement. Taking in account significant morphological differences of *L. fuscus* from other voles of genus, it may be given the taxonomical rank of subgenus.

Distribution patterns of two chromosome forms of common vole (*Microtus arvalis* Pallas) on the common border of their range

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On the territory of the former USSR, the study of common vole (*Microtus arvalis* Pallas, 1779) karyotypes has shown that there are two forms of this species that have the same chromosome number ($2n = 46$) and morphology of macrochromosomes but differ in morphology of small autosome and sex Y-chromosome. It has been established that on the vast range of *M. arvalis* the chromosome forms 'arvalis' and 'obscurus' geographically replace each other. The form with the European distribution was designated as 'arvalis', and with Euroasiatic as 'obscurus'. The hybrids of two forms obtained in the laboratory are fertile. The eastern boundary of the range of the form 'arvalis' and western boundary of the range of the form 'obscurus' are in the European part of Russia and in Ukraine. The major part of the boundary occurs in the country between the rivers Dnieper and Volga.

The main aims of the current work were: clarification of the boundary of distribution of two chromosome forms of *Microtus arvalis*, and study of their distribution in Vladimir and Nizhegorodskaya regions. This territory was chosen because the distance between the extreme known records of the forms 'arvalis' and 'obscurus' comprised only 350 km and the absence of essential geographical obstructions may allow us to find out the possible zone of sympatry.

Within the Vladimirskaya region two forms of common vole that replace each other on the right shore of the river Klyas'ma have been found. On the left shore of this river only one form, namely 'arvalis', was found. The distance between the different forms on the right shore of the river decreased to 12 km in the absence of essential geographical obstacles, and the direct contact between two forms in the Vladimirskaya region seems possible. Preliminary data of experimental hybridisation allow us to propose that the hybridisation of forms 'arvalis' and 'obscurus' in natural conditions is not excluded. However, among the 43 animals analysed we have found no hybrids. Two problems therefore arise: (1) Why do both chromosome forms nowhere meet together? (2) What is the taxonomical status of these forms? We suppose that such distribution is determined by the ethological isolation between these forms. Such isolation between the close species is known, for example sibling species *M. arvalis* inhabiting one territory and even one biotope occupy different microsites in correspondence with the peculiarities of their biology. Seemingly the form 'obscurus' is younger in an evolutionary sense but is essentially biologically similar to the

form 'arvalis'. Furthermore, what prevents them from occupying the same ecological niches? In this case the recognition of individuals of own population from the foreign population is of primary importance and when dispersion is taking place, one form does not let the other form enter its territory. If that is so, the hypothesis should be confirmed that the form 'obscurus' be given species rank.

Study of seasonal survival rates of populations of *Microtus brandti*

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In Zhengxiangbai Banner and Tipus Banner, Inner Mongolia, from 1990 to 1996, seasonal survival rates of two populations of Brandt's vole (*Microtus brandti*) were estimated using capture–recapture methods. Feeding data were derived in the laboratory. During periods when the populations were increasing or decreasing, survival was lowest in winter (mean 0.2473 ± 0.0748) and highest (mean 0.6870 ± 0.1137) in autumn. The number of voles in a burrow system was related to seasonal survival rate, especially in winter.

Migration of rodent species in agricultural landscapes in the Vietnam–Cambodian border region

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In recent years, Vietnamese people living in the border region of Vietnam–Cambodia (Kien Giang, Long An, Dong Thap, An Giang provinces) reported that rats from Cambodia migrated each year to Vietnam around the lunar new year. A study was conducted in the Ha Tien district, Kien Giang province, over two time intervals: from September 1996 to March 1997, and December 1997 to March 1998. A 1.5 km plastic fence (0.8 m high) was established at the Vietnam–Cambodian border. A live-multiple-capture cage trap made of wire (600 × 300 × 300 mm) was placed every 30 m along the base of the fence, flush with an opening to a hole. The live-capture traps were faced alternately towards Vietnam or Cambodia. The traps were checked each day. Rats caught only in the central 1 km of the fence ($n = 35$ traps) were included in the analyses.

In 1996, rats moved from Vietnam to Cambodia (*emigration*) before floodwaters reaching the border region (from the middle of October to the beginning of November). Movement of rats in the other direction (*immigration*) occurred from the middle of February to the beginning of March. In 1998, a similar pattern of rat movements was observed, although the immigration of rats from Cambodia to Vietnam was one month earlier than in 1997 and the peak in immigration occurred in early February.

Almost all the rats were adults. The sex ratio of immigrating and emigrating rats was male biased. The most marked imbalance of females to males occurred in 1998, when twice as many males immigrated than females. The proportion of adult females in breeding condition was generally high. The species composition of rats immigrating and emigrating was markedly different. In 1996–97, 60% of the emigrating rats were *Rattus argentiventer*, 20% were *R. losea* and 20% were a combination of other species, whereas 69% of the immigrating rats were *R. losea*, 20% were *R. argentiventer* and 11% were other species. In 1997–98, 46% of the emigrating rats were *Rattus argentiventer*, 29% were *R. losea* and 25% were a combination of other species. Again there was a switch in species composition for the immigrating rats: 56% were *R. losea*, 28% were *R. argentiventer* and 16% were other species.

We propose that the patterns of migration of rats in the border region of Vietnam–Cambodia are influenced primarily by seasonal flooding of the Mekong Delta and different timing in the cropping patterns on either side of the border. Cropping land in Cambodia is at a higher elevation than in Vietnam, and Cambodian farmers plant only one crop per year. This is a traditional rice variety that takes 6 months to mature. In Vietnam there are two rice crops grown each year, generally they use varieties that mature in 3–4 months. In July–August, the summer–autumn rice crop in Vietnam is harvested when the water level in the delta is gradually rising, forcing rats to move to higher ground. In August–September, rice plants are at the booting to flowering stage in Cambodia. This is a most attractive stage of crop development for rats. In January–February, Cambodian farmers harvest rice then burn the rice straw. In Vietnam, the floodwaters have receded and most of rice crops are at the tillering to booting stages. So again the rats would be attracted to the maturing crops. Why there are seasonal changes in species composition of the migrating rats is not clear. Ecological studies of rat populations on either side of the border are required to understand this conundrum.

What stops population growth in the wild rabbit (*Oryctolagus cuniculus*)?

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Predation, food shortage and disease are thought to be mechanisms responsible for population regulation of the wild rabbit. However, it is unknown whether fluctuations in rabbit density within a habitat can be produced by social processes involving dominance and aggressive behaviour. During a 12-year study, alternative hypotheses of self-regulation of a population within a habitat were tested.

In an enclosure of 22 000 m², a rabbit population stabilised at around 50 adult individuals despite a yearly production of about 400–1200 offspring. From approximately a thousand observation hours, physiological data such as glucocorticoid concentrations, immune-parameters and parasite loads were determined for each individual during their life time. Furthermore, kinship was determined by tagging every individual from the first day of their life within burrows. In addition, paternity was determined by DNA-fingerprinting.

There was evidence of density-dependent suppression of reproduction in females. However, this alone was not sufficient to regulate the population. The survival rate of offspring was related to a density-delayed mortality rate of multi-annual adults. Multi-annual adults were not replaced continuously but in intervals of two or three years.

Wild rabbits lived in small groups of 1–3 males and 1–7 females which were defended against neighbours. Within the groups, there was rank ordering amongst males and females. Social processes like territory extension, formation of subgroups, emigration and immigration of individuals determined the composition and size of a group. The emigration of both sexes probably served as incest-avoidance within the population.

Males regulated and stabilised group size while population size was decreasing by: a) dominant males extending their territories; b) subdominant males replacing deceased dominant males or integrating into groups with many females; and c) males generally guarding their females to prevent dispersal. Females regulated and stabilised group size by: a) emigrating from large groups into smaller groups; and b) maintaining their small group size by becoming territorial.

Group composition related to sex-specific competition and conspecific bonds which acted as a feedback mechanism regulating population density.

Social dominance increased with age, as indicated by a decrease in corticosteroid concentration. Social processes like territory extension, establishment of subgroups and the elevation in life expectancy confirm this hypothesis. Social processes reduced the integration of yearlings, leading to a decrease in population density.

The environmental effects on the distribution of long-eared jerboas (*Euchoreutes naso*)

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The effects of environmental factors on the distribution of long-eared jerboa (*Euchoreutes naso*) were studied in Anxi County, Gansu Province, north-west China, from March to October 1990. Seven sample plots were chosen according to the types of landscape, and were investigated for 5318 trap nights. The population number was calculated by the percent-capture rate. The relationships between the population of long-eared jerboa and environmental factors were analysed using stepwise regression and correlation methods.

The results show that the population of long-eared jerboas is correlated significantly and positively with the total population number of other rodents in the community, and is negatively correlated with the vegetation cover in spring. The optimal standard

regression equation is $Y = 0.314 + 0.345Tc - 0.028D$, $R_t = 0.9845$, ($P < 0.00001$); $R_d = 0.9943$ ($P < 0.00001$). In summer, environmental factors do not significantly affect the population number of long-eared jerboa. However, the population number is correlated positively with the total population number of other rodents in the community. The optimal standard regressive equation is $Y = 0.0941 + 0.0765Tc$ ($R = 0.6992$, $P < 0.05$). It is concluded that the vegetation cover might be the factor determining the distribution of jerboas in super-arid desert areas in Anxi County. The rodents' utilisation of the limited and patchy food resources may be one of the reasons for aggregated distribution of rodents in this area. It is suggested that niche separation in foraging time, food type and size might permit their coexistence.

Rodent and pika populations of south of the former USSR

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Terrestrial animal populations are defined by authors as the total of all animal species inhabiting certain territory. Population maps of terrestrial animals are similar to vegetation maps that reflect distribution of plant communities. Only a few such maps have been published and all of them were for limited regions of the former USSR. Maps compiled by us show modern (1950s–1990s) primary and secondary (appeared on anthropogenically transformed territories) rodent and pika populations of steppe and desert zones and adjacent mountains. The scale of the map is 1:4 000 000. Each community is characterised in the legend by 4–5 indices such as numbers of species, their domination, habitats (predominant and secondary) and some others. A computer variant of the map will be in MAPINFO format and will consist of vector layers with spatial data and databases attached to them. Attached to the contour net of this map there are two tables—a table with a list of species and their numbers and characteristics, and a table with the list of principal and secondary habitats. Included is a map of sites where the material was collected, a table with list of species in each site, geographical coordinates of sites, and bibliographical citations describing these data. The latter enables us to consider the map as the cadastre of communities and species that have been registered within limits of mapped territory.

Predation pressure and population dynamics in African *Mastomys* rats: possibilities for integrated pest management?

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The multimammate rat, *Mastomys natalensis*, is a common and important agricultural pest species in sub-Saharan Africa. The present rodent control relies mainly on the ad hoc use of rodenticides but attempts to design and evaluate alternative

methods are needed. Earlier observations suggest that predation is a major mortality factor in this rodent. In order to investigate the importance of predation for the species' population dynamics and its possible application in biological control strategies, a 3-year study has been set up in February 1998 Morogoro, Tanzania.

The experimental set-up consists of monthly capture–recapture studies of the rodent population in different plots, and monitoring of predator presence by direct observations, trapping and collection of owl pellets. The 0.5 ha field plots are cultivated as maize fields, and subjected to three different treatments (all replicated):

1. excluding predators by fencing and netting the area;
2. attracting predators by improving hunting conditions using perch poles and nest boxes; and
3. allowing predators in unmanipulated situations (control).

A six-month pilot experiment in 1996–97 has shown that perches affect raptors' hunting behaviour and that survival is higher under netted areas but the effect on rodent densities may be obscured by compensating migration effects. To investigate these effects of dispersal the present predation manipulations are repeated both in populations exposed to dispersal (open populations) and in populations without dispersal (enclosed populations).

Seasonal reproductive patterns of the Mongolian gerbil in Inner Mongolia, China

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This study was conducted in Taipus Qi, Inner Mongolia from March to October in 1997. Small mammals were captured at monthly intervals using shaped traps placed in crop fields showing similar environmental characteristics. Gerbil reproductive status was assessed by autopsy.

The breeding peak occurred during March and April. The mass of the testes was greatest in March and April, decreased rapidly in May ($t = 11.35$, $p < 0.001$) and showed no obvious changes thereafter. The epididymis showed similar changes. Seminal vesicle size was greatest in March, and decreased significantly at monthly intervals from March until May ($p < 0.05$ and $p < 0.01$, respectively). No further changes were observed in the remaining months.

The ventral scent gland is an important organ influencing sexual activity. Its length and width are good indicators of testis weight ($p < 0.001$). Body weight also has a high correlation with testes weight ($p < 0.001$).

Ovarian weights of females decreased from March to June. Uterine and vaginal weights increased from March to April, decreased from April to June, then remained

this size. Pregnancies were observed from March to August; 53.5% of females were pregnant in March, 37.5% in April, and about 10% from May to August. The average litter size was 5.88 ± 1.14 (SD).

The Mongolian gerbil shows seasonality in its reproductive pattern with reproduction being concentrated in spring in this region.

Competition between the rat-like hamster and the striped hamster

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The rat-like hamster (*Cricetulus triton*) and striped hamster (*Cricetulus barabensis*) are the two most common species of rodents in farmland in northern China. Competition between the two species was investigated in farmland in Raoyang County, Hebei Province, China. Relative abundance was assessed using more than 440 000 snap-trap-nights from 1983 to 1989. Activity ranges were studied with mark-recapture techniques. Food preference was analysed by examining the contents of cheek pouches of both species.

The results indicated that strong competition exists between the two species. They preferred very similar food items in laboratory tests although food items differed in the field. The rat-like hamster with a larger body mass takes more food (e.g. peanuts, wheat and corn), while the striped hamster with a small body mass prefers the smaller seeds of weeds. This could reduce competition and allow coexistence in farmland. It appears that their niches differ temporally. The striped hamster reproduces in early spring, and reaches peak numbers in spring, while the rat-like hamster reaches peak numbers in autumn. When individuals of the two species fight, the rat-like hamster defeats and often kills the striped hamster.

Population fluctuations of *Microtus fortis* in Dongting Lake area, Hunan, China

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Microtus fortis is one of the main pest rodents in the Dongting lake area. The animals live on the beach of the lake from early fall to next spring. The population increases gradually while the animals live on the beach. In the summer, when the beach becomes flooded, the animals move into the farmland. Usually the animals cause great damage to the crops in the farmland.

The population fluctuations of the animal are different between the beach and the farmland. The key factors influencing the fluctuations are also different.

1. The population fluctuation of the animals on the beach of the lake. The lake beach was the most suitable habitat for the animal. When the lake beach emerged in autumn, the animals moved back onto the beach. The main breeding season was from October to May when the animals inhabited the beach. The population density increased gradually. The duration of the period from when the beach emerged until it again became flooded determined the population size and therefore the number of animals that moved into farmland.
2. The population fluctuation of the animals on the farmland. Farmland was not suitable habitat for the animal. Because of low breeding potential, high mortality and dispersal, the population density decreased during this period. The density of the population in farmland dropped dramatically when the lake beach emerged. The population density on the farmland was very low during winter.

A stochastic model of the responses of farm populations of the Norway rat to anticoagulant use

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In the field every farm appears unique because of the variety of factors that interact to determine the outcome of rodenticide treatments. One approach to such complexity is mathematical simulation. Such a mathematical model has potential to assist with evaluating rodenticide efficacy data and predicting the outcome of treatments which use different materials against populations with varying resistance status.

A model has been developed based on our understanding of rat feeding behaviour, under both controlled conditions in the laboratory and in the field. The core of the model treats as a two-stage process the way animals overcome their initial wariness or 'neophobia' towards rodenticide bait. Firstly, there is the latency for them to first feed on a rodenticide bait. Secondly, there is the subsequent increase in their bait consumption up to an asymptotic value. The size of this asymptote reflects the nature of the alternative food supply; for instance, in a stable environment with abundant alternative food, such as a farm grain store, the asymptote will be low while in an unstable environment with relatively poor quality and limited alternative food, such as a farm refuse dump, the asymptote will be high.

The model has been subject to extensive validation against data collected from the field. The model performs particularly well at simulating the consumption of unpoisoned and anticoagulant baits across a range of farm types and in relation to resistance status. Although the model suggests that more animals are 'killed' during simulations than in the real world this discrepancy is explicable in terms of some factors not included in the model. That the model can make realistic predictions of subtle changes in the resistance status of Hampshire rat populations suggests that it is a robust simulation of the real world.

Population fluctuation of a rodent pest in Yunnan, China

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Mus caroli is an important rodent pest of crops in central Yunnan, China. Among 1027 captures, *Mus caroli* accounted for 76%.

Trapping was conducted monthly in cultivated land in the Tonghai County, Yunnan Province from late 1989 to September 1993. The common abundance index (number/100 trap-days) was determined by using the snap-trap method. Trapping lines were 20 m apart and baited traps were placed at 5 m intervals. The local climate and the development of crops were recorded. All captured rodents were autopsied.

There were significant differences between the average monthly population abundance between different years from 1990 to 1993. The population fluctuation usually peaked twice a year, during May to June and in November. The density fluctuations seemed to be related to the developmental stages of crops and also to the reproductive activities of the rodents.

Two linear and one multiple linear regressions were run to estimate the population abundance in May of the year.

- $Y(M5) = 1.96x + 0.20$, $r = 0.93$
where M5 = population abundance in May; x = population abundance in January.
- $Y(M5) = 2.14x - 21.42$, $r = 0.92$
where x = average of monthly mean temperature during February to March
- $Y(M5) = 1.172 x (I) + 1.1572 x (II) - 12.4848$, $r = 0.990$ ($p < 0.05$)
where x(I), same as formula (I); x(II), same as formula (II).

The population abundance in May of 1994 showed the regressions mentioned above were reliable.

Reproductive characteristics, growth and development of the rat-like hamsters (*Cricetulus triton*)

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Variations in reproduction of rat-like hamsters (*Cricetulus triton*) the most important pest of the cultivated fields, were investigated in Raoyang County, Hebei Province, North China. It was found that reproductive parameters such as length of the breeding season, sexual maturity rate, pregnancy rate, litter size, ratio of resorbing embryos and sex ratio changed as density increased and decreased. Some of the

parameters were inversely related to population densities. During high densities, reduced recruitment, shortened length of breeding season and delayed rates of maturation of the first generation (spring-born) were observed. When population density was at a peak, the rate of growth and sexual maturity were asynchronous. Populations of *C. triton* showed evidence of a strong density-dependent suppression of sexual maturation and a significant negative feedback regulation mechanism. The phenomenon of pregnancy failure in sub-adult females was observed in different seasons during both peak and non-peak years. Sex ratio favoured males over females and was more likely to occur in breeding seasons. It was related to activity and mortality differences between juvenile males and females. The variations of reproduction in relation to air temperature, precipitation, soil type, food supply in different seasons and years were also examined. It is concluded that several reproductive parameters are useful for prediction of population trends.

The growth and development of rat-like hamsters were studied in laboratory conditions. Mean gestation was 21.57 ± 0.69 days and post-partum oestrus occurred by the fifth day. Increases in growth rate were analysed using measurements of weight and linear dimensions. The instantaneous growth rates (IGR) at various ages (from the day of birth to 100 days) showed that the growth was most rapid in the first 10 days. The IGR values at 5–10 days were highest for mass and lowest for body length. From then until 100 days, mass maintained the highest IGR, whereas IGR for hind foot and tail length decreased to very low levels. Sexual dimorphism was not obvious. The morphological and behavioural development of young hamsters was also observed. Weaning occurred at 26.86 ± 1.13 days. Hamsters became sexually mature at the age of 1.5–2 months. Females reached sexual maturity slightly earlier than males. Females had a 3–4 day oestrous cycle. The sex ratio (male/female = 1.71) in captivity favoured males, a result of a higher mortality in infantile females. Development was divided into four periods: infantile period (from the day of birth to 20 days), juvenile period (20–30 days), sub-adult period (30–60 days) and adult period (from 60 days on). Seasonal changes of growth rate were also studied.

Survey of rodents living around Beijing Capital airport

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Beijing Capital Airport is situated in the north-eastern part of Beijing. A survey of rodent species, population densities, habitats and seasonal abundance was carried out using rat traps. For more than 10 years (1984–1994), *Citeilus daurilus* has been investigated by checking holes in the grassland in nearby runways in the area of Beijing Capital Airport. The survey was conducted in three stages. Stage one was the initial survey combined with integrated rodent control (IRC) from 1984–1985. The 2nd and 3rd stages were carried out from 1986–1988 and 1993–1994, respectively.

Seven species of rodents belonging to three families were recorded: *Rattus norvegicus*, *Mus musculus*, *Apodemus agrarius*, *Cricetulus triton*, *C. barabensis*, *Myospalax fantanieri*, and *Citeilus dauricus*. The house mouse (*Mus musculus*) is widely distrib-

uted in the area and is the dominant species making up 62.8%. *A. agrarius*, *C. arabensis* and *C. triton* comprise 17%, 15% and 6%, respectively. The rodent population peaks in September or October every year.

The most effective strategy to reduce rodent infestations is integrated rodent control using poison bait traps, gassing treatments and environmental management. This has reduced numbers from 5.6 to 0.6 rodents per 100 traps, which is less than the infestation threshold level. The average elimination rate was 89% from 1984 to 1985. Environmental factors may also have affected the rodent densities temporarily. However, re-infestation was observed in the area during the 3rd stage of the survey. The infestations increased to 6.0 rodents per 100 traps.

More research is needed to develop methods to effectively and rapidly reduce rodent populations so that their numbers remain below threshold levels.

Symposium B

Rodent Physiology and Adaptation of Rodents

ORAL PRESENTATIONS

Dietary and digestive adaptations of rodents

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Amongst the Mammalia, the rodents are the most diversified order and include the greatest number of species and individuals. Their phenomenal success worldwide can be explained in terms of their generally small size and conservative body plan, their highly adaptable reproductive strategies, and their great dietary flexibility. This paper explores the evolution of rodents from the primitive adaptation of a mandibulo-dental apparatus for an omnivorous diet to more modern forms which include greater specialisation in dietary strategies that include not only omnivory but also strict carnivory (e.g. the Australian water rat *Hydromys*) and strict herbivory (e.g. the Caviomorpha). Four basic characteristics of rodent teeth are rootless, continuously growing incisors with enamel restricted to the anterior face, a large diastema between the incisors and the cheek teeth, the ability to occlude only the incisors or only the cheek teeth, and folds of skin that push inward through the diastema so that the incisors occlude outside the mouth. Because of these features, rodents can efficiently shear vertebrate flesh; stab and seize invertebrate prey; manipulate small seeds; remove bark; and clip off and grind plant stems, leaves and buds.

Evolutionary trends among the rodents as adaptations for herbivory include an increase in the number of transverse ridges on the cheek teeth, hypsodonty, and appearance of continuously growing cheek teeth that develop roots only late in life or not at all; and strengthening of the masticatory musculature; as well as several changes to the gastrointestinal tract. These include an increase in total tract capacity, replacement of unilocular (undivided) with bilocular stomachs; reduction in the proportion of the stomach lined by glandular mucosa and an increase in the area of squamous, non-glandular epithelium; reduction in the relative length of the small intestine; increase in the relative size and complexity of the caecum and proximal colon; and development of a colonic separation mechanism that results in selective retention in the caecum of fluid and small particulate digesta (including bacteria) and in facilitated passage through the colon of large intractable food particles (insect cuticles and plant fibre).

Physiological studies show that rodents can also greatly expand total digestive tract capacity, and rapidly modulate small intestinal hydrolytic activity and nutrient transport capacity in response to peak seasonal energetic demands and changes in food quality. Although functional studies need to be extended across a greater number of

rodent species from a wider range of nutritional niches, it is clear that the great structural diversity in rodent dental and gastrointestinal features is matched by an impressive flexibility in digestive performance. All these features guarantee ecological success and an ability to rapidly utilise new food resources as they become available.

Energetics and thermoregulation of small mammals on the Qinghai–Tibetan plateau

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Energetics and thermoregulation of small alpine herbivores were studied for more than 20 years at a research site located in Qinghai Province, in the northwest of China, about 3200–3500 m above sea level. The climate shows marked temperature differences between day and night but little fluctuation year round. There is a long cold season and a short plant growth period. The species studied were the plateau pika (*Ochotona curzoniae*), Gansu pika (*Ochotona cansus*), plateau zokor (*Myospalax baileyi*) and root vole (*Microtus oeconomus*). The plateau pika and plateau zokor are endemic species, the Gansu pika is distributed in most areas of northwest China, while the root vole has a wide geographical range. The plateau zokor is fossorial, while the others are burrowing species.

1. Basal ecophysiological properties and seasonal variations in metabolism (basal metabolic rate, BMR, resting metabolism, RMR, and average daily metabolic rate, ADMR) were measured.
2. Seasonal variations in non-shivering thermogenesis (NST) capacity were determined and changes in weight, structure, function and chemical composition of brown adipose tissue (BAT) were measured for above-ground active animals. Thermogenic capacities increased during the cold winter.
3. Maximum metabolic rates (MMR) of the plateau pika and root vole were measured and the relationship between MMR and NST, MMR and BMR was analysed.
4. Behavioural thermoregulation of the root vole was investigated. Huddling and nest building are very important for reducing heat loss in root voles.
5. BMR and NST were determined during different reproductive stages.
6. Energetic characteristics during postnatal growth and development were studied in the root vole.
7. Seasonal changes in digestibility and assimilation of natural food were measured, except for the Gansu pika.
8. Cold-induced maximum energy acclimation rate, maximum assimilated energy during peak lactation and the effect of litter size were determined in the root vole.
9. Seasonal variations in digestive tract morphology were observed in four species of small mammals.

10. Effects of photoperiod and temperature on metabolism, NST capacity, MMR, cytochrome oxidase activity of BAT mitochondria, and gut morphology during acclimation were determined.
11. Energy flow through the plateau pika, root vole and plateau zoker populations has been studied. The survival strategies and evolutionary adaptations of alpine small mammals are discussed.

Variations in mitochondrial thermogenesis and expression of an uncoupling protein gene in brown adipose tissue from Mongolian gerbils during cold exposure

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Brown adipose tissue (BAT) is the major site of cold-adaptive thermogenesis in small mammals, and uncoupling protein (UCP) in the inner membrane of BAT mitochondria is the key molecule regulating and limiting thermogenesis. Thus, BAT is very important for small rodents inhabiting the north of China where marked seasonal changes in climate occur. In our study, Mongolian gerbils (*Meriones unguiculatus*) inhabiting northern China, have been selected and raised in the laboratory. Adult gerbils were used in experiments to investigate thermogenic activity and UCP expression of BAT mitochondria during cold exposure.

In adult Mongolian gerbils observed during from 1 day to 4 weeks of cold exposure, firstly the GTP-binding capacity of BAT mitochondria (i.e. indicating thermogenic activity of BAT) increased gradually, and reached its maximum after three weeks. Secondly, there was only one species of UCP mRNA with a length of about 1.5 kb. The UCP mRNA was significantly upregulated after only 1 day, and reached maximum levels after 1 week, then remained at a relatively high level but tending to slowly decrease. Not until 4 weeks was an obvious decline of UCP mRNA content observed. In addition, the specific activity of T45'-deiodinase in BAT also increased gradually. The results indicated that, even during acute cold exposure, the UCP mRNA had been upregulated. Such rapid upregulation of UCP mRNA may be necessary for BAT to synthesise new UCP and to finally acquire its optimal function of thermogenesis. The activation of T45'-deiodinase may be important for the upregulation of UCP mRNA and the recruitment of BAT. Furthermore, the basal GTP-binding capacity of BAT mitochondria is higher in Mongolian gerbils than in rats kept in the same or similar warm environment temperature, indicating higher basal thermogenic activity of BAT. This would be the physiological basis of the high capacity of non-shivering thermogenesis (NST) in Mongolian gerbils. It may be an adaptive strategy of the Mongolian gerbil to large oscillations in daily temperature in its habitat.

POSTER PRESENTATIONS

Seasonal changes of non-shivering thermogenesis in small mammals from an inland semi-arid region on the Ordos Plateau, Inner Mongolia

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Environmental temperatures in the Ordos semi-arid area change dramatically between seasons. It is hot in summer (up to 35°C), and cold in winter (the minimum temperature is -25°C). Temperatures are also low in spring and autumn. To survive these fluctuations in environmental temperature, small mammals may utilise non-shivering thermogenesis (NST) to enhance their tolerance of cold. This study aimed to reveal seasonal adaptations of NST in four species of rodents in the Ordos arid region. The species were the northern three-toed jerboa (*Dipus sagitta*), desert hamster (*Phodopus roborovskii*), striped hamster (*Cricetulus barabensis*) and mid-day gerbil (*Meriones meridianus*).

Injection of a mass-dependent dose of norepinephrine induced NST at 27°C. NST increased significantly in autumn compared with summer values for the four species ($P < 0.05$). In jerboas (a hibernating species) the maximum NST increased 83%, the regulatory NST (NST-RMR) increased 4 times, and the expected NST (NST%) based on body size ($28.9Wb-0.49$) changed from 40% in summer to 73% in autumn. The NST_{max} also showed a 29% increase in gerbils in autumn and the regulatory NST rose 82%.

Desert hamsters showed the greatest variation in NST between seasons. The NST_{max} not only increased 52% in autumn from that of summer, but also was 48% above the summer value in spring. The NST% was 113% and 90% in autumn and spring, respectively, and only 66.1% in summer. The regulatory NST was 2.5 and 2.3 fold higher in autumn and spring than in summer.

In the striped hamster the NST also showed an increase in autumn. The NST_{max} was 53% higher than that of summer and the NST% was 118% in autumn. This species had a high NST in summer, the NST% was 87% and the regulatory NST was 12% higher than the spring value.

A high NST capacity would allow individual jerboas greater tolerance of a cold autumn and be advantageous for accumulation of body fat by reducing maintenance energy expenditure before entering torpor. The small sized desert hamster (15 g) had a high NST both in autumn and spring to tolerate cold temperatures possibly because its micro-habitat is in broad semi-mobile sand dunes where temperatures fluctuate greatly between day and night. The striped hamster, a non-desert species, had a high NST to adapt to the cool habitat, the farmland and the stabilised sand dunes.

Seasonal variation in the digestive tract morphology of four species of rodent in the Ordos semi-arid region, Inner Mongolia

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To understand the strategies used by small mammals for survival in inland arid environments where major changes in temperatures and food resources occur, seasonal variations in the gastrointestinal morphology were studied in four sympatric species of rodents from the Ordos semi-arid region of Inner Mongolia. The animals were the northern three-toed jerboa (*Dipus sagitta*), desert hamster (*Phodopus roborovskii*), striped hamster (*Cricetulus barabensis*) and mid-day gerbil (*Meriones meridianus*). The digestive tracts were measured from snap-trapped specimens.

The results showed that the ratios of wet stomach weight to body mass (SW/BM) in jerboas were 14% and 25% larger in spring and summer than that of autumn, respectively ($P < 0.05$). Similarly the SW/BM were 29% and 47% larger in summer than in autumn in desert hamsters and striped hamsters, respectively ($P < 0.05$). The dry stomach weights (DSW/BM) showed no seasonal changes in jerboas and desert hamsters, but were 41% heavier in summer than in autumn in striped hamsters ($P < 0.05$). The SW/BM and DSW/BM in gerbils did not change with seasons. The ratio of small intestine length to body length (SIL/BL) showed no seasonal changes in the four species. In jerboas, the wet and dry weight of the small intestine (SIW/BM and DSIW/BM) increased 55% and 74% in autumn compared with summer values ($P < 0.05$). In desert hamsters, the SIW/BM also showed the same trend and was 70% heavier in autumn than that in summer. No significant differences were detected in SIW/BM and DSIW/BM in striped hamsters and gerbils between seasons. The ratios of caecum length to body length (CL/BL) were 48% and 64% bigger in spring and summer than that in autumn, respectively, in jerboas ($P < 0.05$). The wet caecum weight did not change with seasons, but the dry caecum weight increased 127% in autumn in comparison with summer values ($P < 0.05$). The CL/BL, CW/BM and DCW/BM showed no statistical differences in desert hamsters between seasons. The CL/BL in striped hamsters was 34% and 21% larger in spring and summer, respectively, than that in autumn ($P < 0.05$), but the CW/BM and DCW/BM did not change between seasons. These three indices of the caecum were not different between seasons in gerbils. There were no seasonal variations in the large intestine for the four species.

These results indicated that the stomach and caecum volume tended to be larger with the additional dietary fibre content in spring and summer.

Energy metabolism and thermoregulation in the desert hamster (*Phodopus roborovskii*) in the Ordos semi-arid region, Inner Mongolia

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The desert hamster (*Phodopus roborovskii*), a small, granivorous rodent (body weight = 15.4 g), was used to study regulation of energy metabolism and body temperature in an inland arid environment. This experiment was conducted in summer (July) 1997 in the Kubuqi semi-desert area of the Ordos plateau. The average air temperature in the shade was 25.3°C, the maximum was 30.6°C, and the minimum was 24.7°C.

Normal body temperature (T_b) was 36.2°C \pm 0.85°C. At ambient temperatures (T_a) of 15–30°C, the T_b gradually decreased to its lowest of 36.5°C \pm 0.86°C at the T_a of 30°C. The equation is $T_b = 38.49 - 0.074T_a$. Above 30°C, T_b increased and reached 40.2°C at $T_a = 36^\circ\text{C}$. The resting metabolic rate (RMR) showed a linear relationship with T_a between 14–28°C and can be described by the equation, $\text{RMR} = 9.73 - 0.228T_a$. The thermoneutral zone (TNZ) was 28–35°C and the minimum metabolism (Mm) was 2.98 \pm 0.65 mL O₂/g.h, which is 164% of the predicted value based on body mass (3.8W_b–0.27). Below 25°C, thermal conductance was 0.321 \pm 0.09 mL O₂/g.h and this changed with T_a in an exponential way. The highest thermal conductance was 2.0 mL O₂/g.h at 36°C.

The high Mm in desert hamsters is different from the general view that desert rodents have a low metabolism to adapt to the heat and shortage of food and water resources in an arid environment. This divergence may be due to stable periods of perennial plant growth and abundant food. Further, a high metabolism is advantageous to animals intolerant of low burrow and environmental temperatures (burrow temperature was 24.3°C at a depth of 58 cm in summer). Increasing metabolism may decrease the lower critical limit of the TNZ and reduce the maintenance energy expenditure. Feeding time and frequency were reduced and this decreased the threat from predators. Below temperatures of 30°C, metabolism decreased, thermal conductance increased and then body temperature decreased gradually. At 30°C, the lowest metabolic rate and body temperature were attained. Between 30 and 35°C, thermal conductance and body temperature increased, whereas the metabolic rate was stable within TNZ. This suggests that the adaptive strategy of desert hamsters in summer, at high ambient temperatures was to increase heat loss to reduce metabolic heat production and enhance heat tolerance. This small, slow-moving rodent has become well adapted to survival in the broad sand-dune microhabitat.

Metabolism and thermoregulation in the Mongolian gerbil, *Meriones unguiculatus*

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The Mongolian gerbil, *Meriones unguiculatus*, is a small cricetid rodent native to the desert and semi-arid regions of Mongolia and northern China. Although there have been extensive studies on thermoregulation of this species, most of the studies were performed on laboratory-raised animals. Marked differences may exist in the eco-physiological characteristics between field and laboratory populations. Therefore, in this experiment we used field-trapped *M. unguiculatus*. Animals were live-trapped in Xilinhot grassland, Inner Mongolia, China, in April 1998. The research site has a broad temperature range between day and night. The rates of oxygen consumption were measured using the Kalabukhov-Skovortsov closed circuit respirometer at a temperature range from 5°C to 40°C. This is the first measurement of metabolic rates over such a wide range of ambient temperatures for live-trapped gerbils.

The lowest mean metabolic rate (BMR) was 2.127 ± 0.140 mL O₂/g.h, which is 173% and 163% of two earlier published estimates, based on body mass. The thermal neutral zone (TNZ) was 26°C to 38°C. Mean body temperature was 37.3 ± 0.5 °C. Thermal conductance below the TNZ was 0.169 ± 0.037 mL O₂/g.h, which is 137% and 133% of that predicted by two earlier studies, based on body mass.

Generally, the typical characteristics for desert small mammals are (1) a relatively low BMR, (2) a steep thermoregulatory curve, (3) a narrow thermoneutral zone, and (4) a poor tolerance for high ambient temperature. Our results suggest that the energy characteristics of Mongolian gerbils are very different from those found in arid adapted small mammals.

Metabolism and thermoregulation in root voles (*Microtus oeconomus*) on the Qinghai-Tibetan plateau

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Ecophysiological properties, such as the level of energy metabolism, will constrain animal distribution and abundance as well as many other aspects of their ecology. Many studies have been concerned with the ecophysiology of microtine rodent species and have shown that high metabolic rates are a significant characteristic of these animals. However, there is no available information for the species that live at high altitudes. Root voles live in the *Potentilla fruticosa* shrub of alpine meadows on the Qinghai-Tibet Plateau. They are a herbivorous, burrowing, winter-active mammal, and face the double environmental stresses of cold and hypoxia. Therefore we postulated that this species should show even higher metabolic levels than other

similar microtine species. Metabolic rates, thermal conductance, and the role of evaporative water loss in thermoregulation were measured in this study.

Animals were live-trapped in the alpine meadow ecosystem, Qinghai Province (37°29'–37°45'N, 101°12'–101°33'E), at an altitude of 3200 m above sea level. The metabolic rates were measured using open-flow respirometry with a Beckman OM-14 oxygen analyser over the temperature range 15–37.5°C. The minimum thermal conductance was 0.30 ± 0.03 mL O₂/g/h/°C, 46% and 52% higher than the values predicted from the allometric equations of two earlier research groups. The width of the thermal neutral zone (TNZ) was 28°C–32.5°C. The minimum resting metabolic rate was 3.29 mL O₂/g/h, 213% and 189% of the values predicted by two earlier studies. Evaporative water loss (EWL) was relatively stable below the TNZ, with an average value of 5.48 mg H₂O/g/h. Within and above the TNZ, EWL increased with T_a, and reached a peak of 13.80 mg H₂O/g/h at 35°C. The contribution of EWL to total thermal conductance was 16% below the TNZ, 28% within the TNZ, 27% above the TNZ, and peaked at 32.5°C at 38%.

These characteristics may have been of adaptive significance for the root vole allowing it to cope with extreme environments where there are large day–night temperature differences, even though average daily temperatures fluctuate little year round. They also suggest that low temperatures may have been a major selective force during the evolution of the root vole on the Qinghai–Tibet Plateau.

Maximum metabolic rate of root vole and plateau pika from the Qinghai–Tibet plateau

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This paper reports studies of seasonal changes in cold-induced maximum metabolic rate (MMR), and its relationships with non-shivering thermogenesis (NST) and basal metabolic rate (BMR) in plateau pikas and root voles.

Plateau pika (*Ochotona curzoniae*, Lagomorpha: Ochotonidae) and root vole (*Microtus oeconomus*, Rodentia: Microtinae) inhabit alpine meadows in Qinghai–Tibetan Plateau. The former is endemic to the area, and the latter has a very wide geographical range in the northern part of Euro–Asiatic continent (Wang and Wang, 1996). Both of the animals are typical small herbivorous mammals.

Winter-acclimatised individuals achieved greater MMR and NST than summer ones, while BMR decreased from summer to winter in plateau pikas and root voles. These results for MMR are reported for the first time. The results of NST and BMR are consistent with results reported previously. The ranges of all metabolic rates are greater in root voles than in plateau pikas. The MMR is 105–111% of expected values in plateau pikas and 137–170% in root voles. Both changes are less than that found in related species from other areas.

There are no seasonal changes in non-shivering thermogenesis (NST) of plateau pika and vole, and this is similar to animals from other regions. NST is very important in MMR, and the increase of MMR in winter results from the increase in NST. The factorial aerobic scope (MMR/BMR) and aerobic reserve (MMR-BMR) in both of the animals are greater in winter than in summer. MMR and BMR for individuals within plateau pika populations in summer and winter were not correlated. However MMR and BMR for root vole were correlated for both winter and summer ($P < 0.05$).

The results provide limited support for the 'aerobic capacity model' for the evolution of endothermy. There is intra-specific variation in MMR and BMR of the two animals. From the metabolic characteristics of small mammals inhabiting the Qinghai-Tibetan Plateau, two life history evolutionary strategies for individuals of these species are proposed as 'increasing MMR' strategy (i-strategy) and 'decreasing BMR' strategy (d-strategy). Individuals with the first strategy have higher MMR, and can survive in much colder environments. Both animals do not store food like related species from Inner Mongolia. Individuals with the d-strategy have lower BMR, and will consume less energy. When the snow is accumulated for several days, which may happen every few years, these individuals will be at an advantage. The i-strategy and d-strategy are the two extremes of evolutionary strategies, which are on a continuum.

Trade-off between reproduction and litter size in root voles

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In this paper, the relationship between energy cost and reproduction of different litter sizes in root voles was studied, and the trade-off between them is discussed.

Total cost (TC), lactation cost (LC) and cost per offspring (OC) are affected significantly ($P < 0.01$) by litter size. TC and LC increased with litter size, and OC decreased with litter size. Total digestion (TD) and total assimilation (TA) increased with litter size ($P < 0.01$), but the total digestibility rate (TDR) and total assimilation rate (TAR) generally remained unchanged. Litter mass at birth and weaning increased with litter size ($P < 0.01$), but mass per offspring at birth remained unchanged and the mass at weaning decreased with litter size.

Offspring production (OP) and offspring production efficiency (OPE) increased with litter size, and production per offspring (POP) and relative energy growth rate of offspring (REGR) decreased with litter size. If the best maternal strategy is to maximise reproduction with the lowest cost, the optimum litter size is the one with largest offspring production per unit cost of offspring. The optimum litter size in root voles inhabiting Qinghai-Tibetan Plateau is five or six.

Effect of photoperiod and temperature on metabolic rates in plateau pikas and root voles

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Seasonal variations exist in maximum metabolic rates (MMR), non-shivering thermogenesis (NST) and basal metabolic rates (BMR) of root voles and plateau pika. Two important physiological factors, temperature and photoperiod, were examined. Root voles and plateau pikas were raised under different environments (temperature: 23°C and 5°C; photoperiod: 16L:8D and 8L:16D hours) with food and water ad libitum.

The effect of photoperiod on metabolic rates. In plateau pikas acclimatised to long or short photoperiods, maximum metabolic rates (MMR), non-shivering thermogenesis (NST) and basal metabolic rates (BMR) remained unchanged. However, in root voles acclimatised to a short photoperiod, MMR, NST and BMR increased significantly ($P < 0.01$) from those acclimatised to long photoperiod.

The effect of ambient temperature on metabolic rates. In plateau pikas and root voles acclimatised to low ambient temperature (5°C), maximum metabolic rates (MMR), non-shivering thermogenesis (NST) and basal metabolic rates (BMR) increased significantly ($P < 0.001$) compared to those acclimatised to warm ambient temperature (23°C).

These results suggest that cold temperature, not short photoperiod, is essential to stimulate the changes in metabolic rates of plateau pikas, but photoperiod and ambient temperature interact to trigger changes in metabolic rates of root voles. The results of root voles support an earlier hypothesis concerning *Peromyscus maniculatus*.

The MMR, NST and BMR of plateau pikas and root voles changed consistently in all acclimatised individuals and between different acclimatised groups. MMR correlated with NST and BMR ($P < 0.05$). The correlation between MMR and BMR support the 'aerobic capacity model' for evolution of endothermy, and this suggest that food plays an important role in the MMR and BMR of animals.

Symposium C

Control Techniques (Biological Control, Habitat Management, Ecologically Based Management, etc.)

PLENARY LECTURE

Rodent pest management in Southeast Asia—an ecological approach

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In Southeast Asia, rodents, insects and weeds are thought to cause similar levels of preharvest losses to rice crops. However, the research effort and basic ecological knowledge on rodent pests lags far behind those of insect pests and weeds. As an indication of their impact, rodents are the greatest agricultural problem in Indonesia, causing annual losses to rice production of 17%. If we could reduce these losses by half, then there would be enough rice to feed an extra 17.6 million people for a year—providing 70% of their energy requirements.

The Australian Centre for International Agricultural Research (ACIAR) is currently funding two projects on the management of rodent pests in rice fields of Southeast Asia. One study is located in West Java, Indonesia (began 1995), the other in the Mekong and Red River deltas of Vietnam (began August 1996). The main objectives are to understand processes leading to increases in rat populations in rice fields, examine how rats use the landscape in these rice ecosystems, and assess the efficacy of using traditional and new methods of rat control. The outputs of the ecologically-based studies are comparable because standard field techniques are being used across these markedly different rice agro-ecosystems.

Currently, chemical control is the primary driver of 'Integrated Pest Management' (IPM) for rodents. This generally provides effective control in the short term, regardless of the rodent species. However, Asian governments are concerned about the affordability and misuse of chemicals, especially when they are striving to provide 'clean and green' food products for their domestic and export markets. The challenge is to build on past efforts of rodent IPM through a better understanding of the ecology of the pest species. This will enable adoption of management actions which are more environmentally sound, sustainable (environmentally and culturally), and likely to be integrated with current IPM programs that are in place for insects, weeds and plant diseases in particular agricultural systems.

This paper will present case studies of current and proposed research to highlight progress and challenges for ecologically-based pest management. One emerging and promising method of control is a trap-barrier system (TBS) for protecting rice crops.

The TBS consists of a rectangular fence with multiple-capture traps inserted at intervals near its base, plus a crop within the fence to attract rats. This crop is 3 weeks more advanced than the surrounding rice crops. It works on the principle that rats enter the water at the edge of the flood-irrigated crop, but cannot gain access to the more advanced crop except by entering a trap. Results will be presented from replicated, control studies that assessed the benefit-cost and optimal size of a TBS.

The TBS plus 'trap-crop' is one of a range of management actions that have been proposed for implementation of EBPM of rodents in Indonesia and Vietnam. These studies will be conducted at the village level and are planned to begin in 1999.

ORAL PRESENTATIONS

Development of fertility control through viral or oral delivery of immunocontraceptive agents: relevance for rodent management

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Management of wildlife pest populations currently relies on methods which increase mortality (e.g. poisoning, disease, trapping, hunting). Fertility control through immunocontraception has been proposed as an additional method which could reduce population size over time. Potentially it could target populations on a large scale, be more humane, and be cost-effective. Such an immunocontraceptive agent could be delivered using either a genetically modified virus or bacterium as the vector, or be delivered in a bait.

We have tested the concept that viral-vectored immunocontraception (VVIC) can be achieved. A laboratory-restricted mousepox virus (ectromelia virus), has been engineered to express an oocyte-specific antigen, the mouse zona pellucida 3 (ZP3) glycoprotein. Female mice (BALB/c strain) infected with the recombinant ectromelia virus produced antibodies against ZP3 and were infertile for 5-9 months. In about half of the animals, infertility was associated with disruption of early follicular development in the ovary, but with no evidence of inflammation (oophoritis) in ovarian tissue. For the remaining animals, antibodies coating mature oocytes could have prevented fertilisation by inhibiting sperm binding to ovulated eggs or penetration of sperm through the zona. Mice became fertile as ZP3 antibody levels in the serum decreased. Reinfection of the mice with the recombinant virus boosted the anti-ZP3 response and also restored infertility.

Recently, we have also achieved similar results using another mouse-specific virus, mouse cytomegalovirus (MCMV), which occurs naturally in the Australian environment. Currently this virus is considered to be the best candidate for eventual field use of VVIC. MCMV has also been engineered to carry the mouse ZP3 gene. Female BALB/c mice infected with recombinant MCMV-ZP3 (MCMV-ZP3) have remained

infertile for at least 170 days and have high serum levels of anti-ZP3 antibodies. The immunocontraceptive effect has been also demonstrated in A/J mice and a partial effect seen in the outbred ARC/s strain and C57BL/6 mice. In addition, mice infected with parental virus become infertile when subsequently infected with the MCMV-ZP3. This suggests that pre-existing immunity to MCMV does not preclude reinfection with MCMV-ZP3 and this is able to result in subsequent immunocontraception in BALB/c mice. The mechanisms of MCMV-ZP3 induced immunocontraception are currently being investigated.

We are also developing bait-delivered vaccines for foxes in Australia and this approach may be suitable for strategic management of rodent populations.

Viral-vectored immuno-contraception as a potential control strategy for house mice in Australia

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The house mouse (*Mus domesticus*) is a significant problem in the grain-growing regions of eastern and southern Australia because of its ability to rapidly increase to densities of around 1000 mice per hectare. These mouse 'plagues' cause economic and social hardship in rural communities, ultimately resulting in impacts which are felt nationally. Current methods for managing mice in Australia include the use of poisons and modifications to farming practices. However, on their own, these management strategies are often not sufficient to halt increases in mouse numbers. Furthermore, some of these techniques have potential impacts on the environment that preclude them from being used as long-term control strategies.

An alternative and more appropriate approach is to reduce the reproductive potential of mice. House mice are prolific breeders, with one pair theoretically capable of producing 500 mice in 21 weeks. One way of achieving a reduction in fertility, is by using a method called viral-vectored immunocontraception (VVIC). This approach relies on inducing an immune response in the pest animal against species-specific reproductive proteins, thus blocking fertilisation. The sterilising protein is delivered using a species-specific virus which would disseminate through a wild population causing infertility in infected mice.

Experiments simulating the effect of immunocontraception on mouse populations indicate that a level of 67% sterility amongst females is sufficient to significantly reduce population size. These simulations were achieved by surgically sterilising females in mouse populations housed in near-natural outdoor enclosures. Results suggest that it is important to maintain this sterility level over more than two generations. It would be easier to maintain or pass on sterility to each generation using a disseminating system such as VVIC, rather than by using repeated baiting with a non-disseminating immunocontraceptive bait.

The ability to predict the likely behaviour of a sterilising virus in field populations relies on an understanding of the epidemiology of the vector virus in wild mice. The virus that we propose to use is murine cytomegalovirus or MCMV. This herpes-type virus is mouse-specific and is already present in wild house mice in Australia. It is spread by close contact and produces a persistent, non-lethal infection. Multiple infections with more than one strain of the virus are known to occur in a single mouse. Therefore, MCMV is an ideal candidate for a viral vector. However, there is still much to learn about this virus in wild mouse populations and this is the focus of new research. The key population-scale questions to be addressed are:

1. What is the transmission rate of wild and recombinant strains (including a sterilising strain) of MCMV in wild mouse populations? What population parameters influence transmission rate?
2. Can a recombinant strain of MCMV establish and generate an immune response in a mouse population which has already been infected with wild-type MCMV? Is the order of infection important?

We will also obtain some information on the dynamics of MCMV infection in wild mice, the importance of sexual transmission, the likely persistence and infectiveness of MCMV in the environment and the threshold population size required to maintain MCMV infection.

Urban rodent control programs for the 21st century

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Urban rodent control in the U.S. historically has been implemented in a limited or disjointed fashion rather than comprehensively, and programs commonly have been reactive rather than proactive. Reasons for this have included limited funding, training, and political and technical support. As urban infrastructure ages and congestion increases, the need for effective rodent control programs will become even more important for both public health and economic reasons. Additionally, expectations of urban residents and businesses for quality-of-life improvements will continue to grow.

Urban rodent control for the 21st century must focus on a program approach that is both strategic and comprehensive. This must include effective long-term planning, scheduling, data management, and mapping capabilities. It also must focus on greater partnership among municipal agencies, private pest control companies, and community groups. Central to program success will be coordination, communication, and accountability among all program participants. Cost-effectiveness will be achievable, but predicated on effective administrative management and training. Greater focus on infrastructure maintenance and construction will be essential for long-term removal of factors that enhance pest problems.

A comprehensive program in Boston, Massachusetts over the past 10 years has demonstrated many elements needed as part of future urban rodent control programs. This has included pest control companies with well-defined contract specifications, city agencies with well-coordinated roles, involvement of residents and businesses, and program managers with technical and administrative training. Through an intensive initial effort, followed by a maintenance program, Norway rat (*Rattus norvegicus*) populations in both surface and subsurface (utility) environments were dramatically reduced and consistently managed.

Key program elements in Boston included neighbourhood organising and education, improved regulatory enforcement of sanitation codes, improved refuse containment, strategic use of rodenticide, an effective sewer baiting program using brodifacoum, alteration of urban landscaping, infrastructure repairs, use of monitoring tools such as census bait, and review of future infrastructure designs to incorporate rodent control principles. A team approach was the program's foundation, ensuring that all aspects of rodent control were centrally coordinated, and that problem resolution was comprehensive and efficient.

Integrated management of the rice field rat (*Rattus argentiventer*) in West Java

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This paper discusses the concept of integrated pest management (IPM) and considers the progress that has been made towards effective implementation of IPM for rodent pests in agricultural systems in Jatisari, West Java.

Integrated management of the rice field rat was conducted during planting time in 1990–1991 at the Jatisari Forecasting Center in West Java, on a 40 ha area of local farmland including the Jatisari experimental field. Habitat management in the form of synchronous planting of rice and elimination of rat refuges was conducted initially. Fumigation, chemical control by rodenticide, and a combination of plastic fences and multi-capture traps (here after referred to as PMT) were subsequently used to control rats. The total number of rats killed by these methods reached 3981 (3546 rats by PMT, 31 by single-capture traps, 94 by fumigation and 310 by chemical control/rodenticide). Rat damage in the field was reduced by over 99% (down to 0.2% damage).

Effective methods for controlling the rice field rat population before planting time were to synchronise planting, eliminate refuges for rats and to burn straw after harvesting. During the planting season PMT was used in the seedbed and the trapping crop area (an area planted one month earlier) to control the rice field rat population. PMT was also used for preventing the immigration of rats from surrounding areas during the generative stage of rice growth.

Effective methods for controlling rat populations during land preparation, ripening stage and after harvest were to fumigate and dig out burrow systems of rats on the dikes. The efficacy of fumigation and digging burrows is about 60% during peak population density. The application of rodenticide was effective from tillering to the end of maximum tillering under certain conditions.

Overall, PMT was found to be the most effective method for controlling the rice field rat population in paddy fields.

Population ecology of the rice field rat, *Rattus argentiventer*: implications for management

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The rice field rat, *Rattus argentiventer*, is one of the most important preharvest pests of rice crops in Southeast Asia, accounting for an annual loss of 17% in Indonesia. We recently conducted a capture-mark-recapture study to identify important factors limiting populations of this rodent. This knowledge will be used as a basis for designing management strategies for the pest.

The study site was located in irrigated lowland rice fields in Sukamandi, West Java, Indonesia. Two rice crops were grown each year: the wet season crop from mid-October to February; a short fallow in March; the dry season crop from April to July; and a long fallow from August to early October. The main crop growth stages are tillering (55 days), reproductive (35) and ripening (30).

Trapping was conducted using eight trap lines once every three weeks from April 1996 to April 1998. At each trap line, eight multiple-capture cage traps were set 20 m apart along a drift fence for three consecutive nights. Captured animals were individually identified, sexed, weighed, breeding condition assessed, and body dimensions measured, before being released at the point of capture. Newly-captured animals were marked by a uniquely numbered ear-tag. Crop stage and other factors were recorded at each census.

A total of 3660 rats over 8688 trap-nights was captured. Recapture rates within and between censuses were low. The number of rats captured per trap line was used as a measure of population abundance.

Mean abundance was significantly lower in the middle of paddies than in paddy margins at most crop stages, indicating that populations are limited by the availability of nest sites. Rats only nested in burrows in levee banks when rice fields were flooded. Mean abundance and body condition of rats were lowest at the mid-tillering stage after a 3-month fallow in the dry season. These declines are possibly due to the reduced food supply during the fallow.

Based on the dates when pregnancies and new born litters were detected, we deduced that mating begins as early as the late tillering stage allowing up to three litters per female over the nutritious ripening stage of crops. Mean population abundance was increased through the subsequent influx of juveniles and sub-adults during the late ripening and early fallow stages. This coincidence indicates that reproduction and population growth may be limited by high-quality food supply.

We recommend the following management strategies for critical trials: (1) minimise the number/size of levee banks and maintain/retain the long fallow to limit populations; (2) synchronise crops to minimise breeding period; and (3) time application of mortality control at the mid-tillering stage when populations are low and least capable of compensation.

Current trends in rodent damage management for Hawaiian agriculture and conservation

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Introduced rodents have caused, and continue to cause, substantial economic and ecological damage to the Hawaiian Islands. Due to the impact of these species, significant effort is being expended to understand their biology and control. Four species of commensal rodents are currently found in urban, agricultural, and natural habitats in the islands. These species are the roof rat (*Rattus rattus*), the Polynesian rat (*Rattus exulans*), the Norway rat (*Rattus norvegicus*), and the house mouse (*Mus musculus*).

In Hawaii, interest in rodent control in Hawaii historically was associated with human health issues (bubonic plague) and the need to reduce crop losses to rats in sugarcane. In recent years substantial research efforts have been devoted to development of techniques to manage rodent damage in macadamia (*Macadamia integrifolia*) orchards and in conservation situations. As land-use patterns change in Hawaii other problems with rodent depredations, for example in agroforestry, may emerge.

Roof rats (*Rattus rattus*) damage an estimated 5 to 10% of the developing nut crop in Hawaiian macadamia orchards. Aspects of roof rat biology in macadamia orchards are studied with the ultimate goal of developing an ecologically sound and cost-effective integrated pest management plan. I will present data which suggest that: 1) roof rats are the primary rodent pest species of concern for macadamia producers; 2) broadcast baiting of rodenticides on the ground in macadamia orchards without interior vegetation is ineffective for roof rat control; and 3) macadamia trees can compensate for rodent damage early in the crop cycle. Efforts are being made to obtain a state registration for anticoagulant rodenticide use in bait boxes in macadamia trees.

Rodent control is considered a high priority for many species and ecosystem restoration plans in Hawaii. Broadcast rodenticides have been used successfully to control introduced rodents for species conservation in New Zealand and could potentially be used in Hawaii. This apparent success caused biologists in Hawaii to seek regulatory approval for the use of similar techniques in this State. In 1995, a State registration for the use of 0.005% diphacinone bait blocks in bait stations to reduce rat depredation in native Hawaiian ecosystems gained approval. At present, wildlife management agencies in Hawaii are gathering the appropriate information for similar registrations for the aerial broadcast of rodenticides in Hawaiian conservation areas.

Rodent management in Vietnam

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Rodent pests are an increasing problem in agro-ecosystems in Vietnam. However, little is known about which rodent species are responsible for losses in crop production, let alone how best to manage their impact. This paper will report on a 2-year ecological study of the rice field rat, *Rattus argentiventer*, in the Mekong River Delta of Vietnam. Rats were live-trapped (capture–mark–release) in a range of representative habitats based in and around the rice growing region of Tra Vinh Province. Traps were set in rice crops (two or three rice crops per year), main channel banks, vegetable plots, banana and coconut plantations, melaleuca forest and undisturbed grassland. Supplementary kill-trapping was conducted to determine the breeding status (per cent adult females breeding, litter size and development) of the rats and to confirm their taxonomy.

In the Tra Vinh rice ecosystems, the dominant rodent species were *R. argentiventer* (60%) and the lesser rice field rat, *R. losea* (15%). Eleven other species made up 25% of the population—each was considered a minor component of the population and unlikely to cause significant damage to preharvest rice. We report on the breeding patterns of the two main rodent species during the wet and dry seasons, and the relative dynamics of rodent populations in the different habitats during these seasons.

Our focus on the ecology of the key rodent pest species has helped to define a range of potential management practices that should be environmentally sustainable, economically feasible and socially acceptable. The challenge ahead is whether these actions will be readily adopted at the village and/or district level. Concurrent implementation of management activities is an essential requirement for mobile species such as rodents, which can readily invade small areas following a reduction in rodent densities.

Preliminary study assessing integrated rodent management strategies for soybean crops in Thailand

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In the most regions of Thailand, soybean crops grown in the dry season (January–April) experience rodent damage. Most farmers address these problems by using large quantities of pesticides, which can also have major impacts on non-target species. Farmers use bow traps to reduce their use of rodenticides but the effectiveness of these traps as part of an integrated rodent control is untested.

The objective of this study was to assess proposed integrated strategies for control of rodents by testing the effectiveness of a combination of the use of bow traps and the acute rodenticide, zinc phosphide. The experiment was conducted in 10 study plots of soybean grown at the end of December 1997 and harvested in April 1998. Each plot (about 0.6 ha) was located in Nhong Wua So district, Udon Thani province, about 550 km northeast of Bangkok.

Five experimental treatments were undertaken, each replicated twice. These were: (1) bow traps alone; (2) 1% zinc phosphide bait alone; (3) bow traps and 1% zinc phosphide bait; (4) normal farmer practices of rodent control; and (5) no rodent control. During one crop season, each treatment was applied at three different crop stages: soil preparation before planting; flowering (\approx 40–50 days after sowing); and young pod stage (70–80 days after sowing). Before each period of treatment, the populations of rodents were measured using a footprint index and bait consumption.

Counts from the footprint index and the number of rodent carcasses in the bow traps showed that the most abundant species throughout the crop season were the fawn-colored mouse (*Mus cervicolor*), the Ryukyu mouse (*Mus caroli*) and the lesser rice field rat (*Rattus losea*). The great bandicoot (*Bandicota indica*) was observed (footprint index) to be more abundant during the flowering stage through to harvest.

The weight of seed damaged by rodents in three of the treatments (bow trap alone, zinc phosphide alone or the combined treatment) were at a similar level (91.6–134.1 kg/ha) but were quite different from farmers' plots (197.5 kg/ha) and the no-rodent-control plots (730.6 kg/ha). Results were analysed using analysis of variance and Duncan's New Multiple Range Test.

It is concluded that bow traps could be a suitable alternative method for controlling rodents in soybean fields where *M. cervicolor*, *M. caroli* and *R. losea* are abundant. This could reduce rodenticide use for rodent management in soybean crops in the dry season.

Rodent management in Qinghai–Tibet alpine meadow ecosystem

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In Qinghai–Tibet Plateau there are about 1.5 billion ha natural grasslands which are widely distributed in the east of the plateau and on high mountain ranges. Alpine meadow, which covers 49% of the total grasslands area (16 million ha) in Qinghai Province, is an important area for animal production, but is seriously damaged by rodent pests. The dominant pest species are the plateau pika (*Ochotona curzoniae*) and plateau zokor (*Myospalax baileyi*). Their foraging and burrowing activities increase degeneration of the grasslands and secondary bare areas are formed. Many scientists are studying rodent biology and ecology to develop better management of rodents in the alpine meadow ecosystem.

With increasing population densities of both species from spring to autumn, damage to the grassland is aggravated and there is a significant decline in the yield and coverage of good foraging grass. A significant correlation has been found between rodent numbers and the damage to vegetation and so an economic threshold for controlling rodents can be established according to the degree of overgrazing and degeneration. Currently, a vicious circle occurs in the grasslands with overgrazing leading to degeneration, then increased rodent numbers leading to further degeneration. However, if the densities of the pest rodents can be constrained and the ratio of excellent forage grass increased so that the density, coverage and height of vegetation increases, then this is effective for controlling plateau pika.

Since the 1960s, many rodenticides have been used in Qinghai Province. From their intensive studies on ecology, behavioural ecology and behaviour of the rodents, Institute scientists have developed a simulated burrowing poisoning machine that takes advantage of the invading behaviour of zokor. A major response was achieved after a single poisoning with the number of the pika and zokor reduced to less than an economic damaging level. Integrated control was demonstrated on 800 ha of secondary bare area using a series of treatments including chemical control with the machine, seeding, fencing, grazing and weed control. Within 3 years the vegetation recovered and productivity increased with 2000 t of dried forage grasses produced in the treated area.

Ecological management of Brandt's vole in Inner Mongolian grassland, China

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Brandt's vole (*Microtus brandti*) is a pest in the grasslands of Inner Mongolia where it populations accelerate degeneration of these grasslands. Control of this pest through ecological management is an urgent problem.

Brandt's vole avoids habitat where vegetation is higher than 16 cm. Most of its food is from dicotyledons which are also stored as a main food source for winter. May is an important month for grass growth. The custom in this region is to fence alternative areas in late May for autumn harvest or winter grazing.

We sowed *Aneurolepidium chinense* seeds in spring to increase the proportion of monocotyledons in plant communities and to decrease the preferred food of Brandt's vole. Degenerated grass areas were fenced in early May, two weeks earlier than the custom in the region. This resulted in a high cover of vegetation, and increased the proportions of monocotyledons in the plant community. These conditions reduced social and living conditions for Brandt's vole.

Through these ecological measures we achieved high quality grass for livestock and controlled Brandt's vole density at low levels for an extended time. To avoid pollution in the environment no chemicals were used.

Ecological management of voles (*Microtus brandti*) and pikas (*Ochotona daurica*) in Inner Mongolian grasslands

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Changes in the communities of rodents correlates with degeneration of grassland. The pika occurs when there is slight degeneration of grassland, while vole outbreaks occur during intermediate degeneration of grassland. By fencing in early May to protect the vegetation from grazing, the improved vegetation suppressed the density of voles, but increased the pika population.

Observations indicated that pikas harvest plants for winter food in autumn, and press the plants into store-piles beside the holes. This storing activity begins in the middle of autumn and continues until the first snow falls. The study showed that pikas would not store food after the first snow falls even though the food stored was insufficient for the length of the winter. The main components of the food and store-piles were dicotyledons. The storing activity therefore strongly influences the survival of the pikas.

Fencing degenerated areas of grassland from early May, sowing *Aneurolepidium chinense* and *Agropyron cristatum* seeds in spring, and harvesting grassland before the beginning of pika storing activities, eliminated the store-piles beside the pika holes just before the first snow falls. After these treatments, we increased the harvesting of the grass and, by increasing the proportion of monocotyledons in the plant communities, decreased the capacity of pika and vole populations to increase simultaneously. Both populations were controlled over a long period. This management regime achieved both the suppression of the populations of the two rodent pests and improved the grass harvest for livestock. This result showed high economical efficiency without any contamination with rodenticides.

Ecologically based rodent management in Africa: no quick solutions for urgent problems

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Rodent management in Africa is generally organised ad hoc for control of acute problems. Nearly always, the approach is based on rodenticides, with the choice of poisons being dictated by availability rather than efficacy. Alternative strategies are used locally on a trial and error basis but the biological basis for these approaches is usually rather poor and controlled experimental designs are not commonly applied.

In this paper, I present several possible field rodent management strategies and discuss how well their application is supported by the available ecological information. For most examples, I will use data that were collected in a population of *Mastomys natalensis* in Tanzania. The use of population models as a formalised way of using the available knowledge will be illustrated.

The focus is on:

- symptomatic lethal control
- periphery baiting with rodenticides
- prophylactic lethal control (avoiding damage to crops)
- preventive lethal control (avoiding build-up of rodent populations)
- environmental control by weeding, burning etc.
- trap crops, social fences
- biological control with predators
- contraception.

Unfortunately, the available ecological information does not allow for much optimism with most of these approaches. In order to test new strategies, specifically designed experiments are proposed. However, each of these will require considerable amounts of field work and solutions are not to be expected very soon.

Chronobiology applied to rodent pest management—the case of semi-arid agriculture in sub-Saharan West Africa

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Chronobiology studies the mechanisms which allow species to react and adapt to the variations of their environment. In mammals, daily and seasonal variations of certain environmental factors called synchronisers (e.g. day–night alternation, photoperiod, temperature, relative humidity, food resources, chemical signals, pheromones and rodents density), are perceived by certain structures of the brain (e.g. suprachiasmatic

nucleus and pineal gland). Thus informed on the progress of days and seasons, the brain is then able to integrate environmental factors with:

- day–night alternation, to influence a great number of daily behaviours (locomotor, food, exploratory, etc.);
- seasons, to influence a great number of seasonal physiological functions (reproduction, mobility, metabolism, etc.).

I present our methodological approach, which comprises three stages (correlative study, causal study and modelling), and some cases studied in Burkina Faso and Mali (on *Arvicanthis niloticus* in stable wet habitats or in flooding habitat; *Taterillus gracilis* in semi-arid habitats and *Gerbillus nigeriae* in arid habitats). These results show that daily behavioural rhythms and seasonal vital functions are specific and allow species to anticipate (at the behavioural and physiological levels) the arrival of daily and/or seasonal ‘favourable’ and ‘unfavourable’ periods. Knowing these daily and seasonal rhythms/cycles is very useful for rodent pest control, because it determines, for example, if periods are favourable or unfavourable for use of anticoagulants, which in turn influences the risk of developing resistance. Knowledge of the mechanisms which determine daily rhythms and seasonal cycles is also essential for identifying the climatic and/or trophic situations which perturb the internal mechanisms of regulation of rodent populations such as reproduction and mobility. These can lead to demographic collapse or to reproduction-dependent and/or mobility-dependent outbreaks. The chronobiological approach is therefore complementary to the ecological approach, and allows us to find specific spatial and temporal strategies for rodent pest control.

Rodent pest control in relation to population organisation

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The population structure of rodents may significantly influence the effectiveness of pest control activities and the success in decreasing the natural foci of rodent-borne diseases. We studied population reactions of 16 species of small mammals in relation to this problem. Experiments were conducted to examine the organisation of natural populations and the response of populations after control was applied. Also, we collected data on the population reactions under natural catastrophes (for several species). The parameters studied were: space use; social behaviour; dispersion; breeding; and rate of re-establishing.

Using the ratio of the term of re-establishing to the period of recruitment by breeding (mating – dispersion of young animals) we can divide all species into ‘fast’ and ‘slow’ re-establishing species. The species that were ‘fast re-establishers’ had their rate of re-establishing overlapping the rate of breeding. It is obvious that such re-establishing can be provided by immigration only. We studied population organisation in ‘fast re-established species’ and found that a high rate of dispersion in populations was related

to different population structures. It is more useful then, to analyse not the definite population structures but the mode of function. Several population traits were correlated with function. For the 'fast' re-establishing species: high rates of change in casts (over 30% for 60 days) and high ratio of dispersers in daily capture (over 30%). For the 'slow re-established species they were: high stability of the cast (less than 8% of changed individuals) and low ratio of dispersers (less than 5.5%). Among species with 'fast'" re-establishment there were animals that provided only one mode of function and those which provided the mode of function in relation to the conditions. In order to analyse them, we introduced the terms 're-establish function' (rf) for the metapopulations provided fast re-establishing, and 'control function' (cf) for those that provided slow re-establishing (in the last case provided self regulation of density). Thus, three groups of animals could be distinguished, based on differences in the functional organisation of populations. The first group consists of animals which can provide both rf and cf. They change the mode of function and increase their dispersion activity after changes to their environment (e.g. pest control procedure). It leads on one hand to a decrease in pest control effectiveness, and on the other to an increase in the probability of contacts with sick animals. The second group of species provide only rf animals. They did not achieve a high density as a rule, but they are resistant to pest control and may be a significant factor in dispersion of natural foci of diseases. The third group of species provided only cf animals. They are numerous in the natural environment but they are the most sensitive to pest control.

Bark-stripping of tankan orange, *Citrus tankan*, by the roof rat, *Rattus rattus*

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Roof rats, *Rattus rattus*, damage the bark of tankan orange, *Citrus tankan* Hayata, over a wide area of Amami Oshima Island, in the Nansei Islands in southern Japan. Farmers have been engaged in tankan cultivation for about 30 years. This study examined the food habits of the roof rat to determine whether they are responsible for early bark stripping of the tankan trees.

Amami Oshima (28°10–30'N, 129°10–45'E) is an island situated in the subtropical climate zone with an area of 712 km². The climate is warm and humid, with an annual rainfall of 2871 mm. In mid -September 1997, I carried out a study at a tankan orchard.

I confirmed that the tankan trees were attacked by roof rats based on their tooth marks on trees and their hairs in faeces dropped under trees. Most of the damaged trees were completely girdled. Some 21 rats were collected by 90 snap-trap nights around the tankan orchard.

Phloem of tankan, which was identified by the characteristic sieve areas of the tissue, was found in 2 (11%) of 18 stomachs of the rats examined. However, no trace of outer bark was found in those stomachs. Clearly, the rats chewed the phloem con-

tained in the bark chips, because there were tooth marks on the inside of bark chips as well as on the tree surface. The rats seemed to have digested the phloem incompletely and absorbed only the sap because their faeces were filled with the phloem fibres. Seeds and fruits, including 6.4% of an immature tankan fruit, accounted for 30% of the stomach contents in volume, whereas the phloem accounted for only 9%. These results show that the primary vegetable foods of the roof rats were seeds and fruits and that the phloem was not a substitute food source. I conclude that roof rats stripped the bark of the tankan orange to obtain the sap in the phloem, although the reason for this activity remains uncertain.

Towards an ecological approach for management of plague reservoirs and vectors in the western Usambara Mountains in Tanzania, East Africa

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Outbreaks of human plague in the Western Usambara Mountains in Tanzania are strictly seasonal, occurring between October and June each year since 1980. Studies have been carried out in the past to elucidate the breeding patterns of rodents, population densities and the species involved as reservoirs and vectors of the disease organism. The studies have involved removal trapping of animals and determination of rat population densities and flea abundance on rodents. In the current study, a review of the data collected in the past was carried out to establish the appropriate ecological approaches for management of both reservoirs and vectors of plague.

A hypothesis is provided to explain the increase in numbers of plague cases between October and June. The studies suggest that favourable temperatures (22–26°C) and humid conditions between November and March favour rapid multiplication of fleas, thus increasing their abundance on rodent hosts. This period coincides with increasing numbers of wild, peri-domestic and house rodents. The chance of house-infesting rodents, mainly *Rattus rattus* and peri-domestic species (predominantly *Mastomys natalensis*), picking up infection from sylvatic species increases several fold. This enables the disease to be transferred from wild rodents to man. The onset of the heavy rains (March–April) and the cold and dry conditions (May–September) lowers the flea abundance and arrests the spread of the disease during this period.

An ecological approach on an area-wide basis to control both vectors and reservoirs of the disease to supplement the conventional techniques using rodenticides and insecticides has not been attempted. A comprehensive management strategy should involve habitat management approaches, enforcement of environmental sanitation to remove sources of food and reducing potential areas for rodent harbourage and breeding, especially for *Arvicanthis niloticus* and *M. natalensis*. Sanitary improvements and cleanliness in houses to reduce house-infesting fleas and populations of *R. rattus* are necessary.

Finally, a better understanding of the ecology of reservoirs and vectors of plague through continuing studies is mandatory for their successful management.

A promising new approach in muskrat control (*Ondatra zibethicus*): the introduction of eradication standards

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The muskrat, *Ondatra zibethicus*, can cause substantial damage to banks of watercourses and crops by its gnawing and burrowing behaviour. Eradication of this exotic animal was legislated in 1938. A general reporting and elimination duty still exists in Belgium. Regional, provincial and municipal authorities organise muskrat eradication programs along the watercourses which fall within their jurisdiction. The total costs for muskrat destruction in Flanders (North Belgium—area 13 522 km²) can be estimated annually at US\$15–20 million. One of the aims of this research is to reduce eradication costs by optimising muskrat control.

A closer look into the practice of elimination of the muskrat, in which several hypotheses were experimentally checked, reveals that a properly conducted eradication program results in a very thorough ridding of an area or watercourse. On the other hand it appears sometimes that for one reason or another small areas remained unprocessed. In some cases densities of muskrat exceed 150/km².

We demonstrated in a field experiment that local residual populations were able, within a short time, to re-colonise the surrounding areas. The main problem appeared to be the thoroughness with which potential refuges were localised, rather than inefficient use of rodenticide (chlorophacinon) or of the different types of mechanical traps.

The following quality standard for a successful muskrat control was therefore formulated: no residual populations with a density exceeding a pre-set number of animals may be found within a processed area (i.e. may be localised during an inspection). The standard limit was fixed at 5 MR/km² (January–March), 10 MR/km² (April–June), 15 MR/km² (July–September) and 10 MR/km² (October–December).

Our research was closely monitored by the Department of Water of the Flemish Government and in 1996 a long-term experiment on muskrat eradication was organised in five areas (total area 2633 km²) in which the new quality standard (eradication goal) formed the core of the experiment. In addition, a supervision and evaluation system was devised in connection with the eradication programs. This new approach has already resulted in promising eradication figures of muskrats.

Use of *Sarcocystis singaporensis* as a biocontrol agent against the Malayan wood rat, *Rattus tiomanicus* in oil palm plantations in Thailand

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The coccidian protozoan, *Sarcocystis singaporensis*, naturally occurs in skeletal muscles of the Malayan wood rat, *Rattus tiomanicus*, which is a chronic pest in oil palm plantations in Thailand. Previous tests on the pathogenicity of this parasite performed by the Agricultural Zoology Research Group, Department of Agriculture, showed that sporocyst doses of $>1 \times 10^5$ were lethal to rats within 11–19 days. The purpose of the present study was to test the effectiveness of *S. singaporensis* against the Malayan wood rat under field conditions.

The experiment was conducted in oil palm plantations in the southern part of Thailand. Four fields were randomly allocated to two treated and two control plots. Each plot consisted of 20×20 palm trees (3.24 ha). Baits containing 4×10^5 sporocysts/pellet or placebo-pellets were offered in 2 rounds, 15 days apart. Three pellets were placed at the base of each tree during the first round; two pellets per tree were applied in the second round. In core areas comprising 10×10 palm trees, rat numbers and rat activity were recorded before and after treatment with parasites and placebos. Rat numbers were determined in three traps nights with 100 live-traps per night. Footprints were counted by tracking plates marked with black ink and evaluated by using a transparent grid of 16 squares. A total of 150 plates was used in each plot. The core areas were extensively examined for presence of dead rats 13–15 days after each application of parasites.

At 11–17 days after the Malayan wood rats had consumed parasite-pellets, their numbers were significantly decreased by 71% compared with the control groups ($\chi^2 = 35.3$, $df = 3$, $P < 0.001$). Activity inside the parasite-treated plots was also significantly reduced compared with controls ($\chi^2 = 24.8$, $df = 3$, $P < 0.001$). We conclude that Malayan wood rats can be effectively controlled by artificial infection with *S. singaporensis* in Thailand.

POSTER PRESENTATIONS

Ecological and socio-economic factors influencing integrated rodent management (IRM) in rural areas of Yunnan, China

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Integrated rodent management (IRM) was adopted in 1985 in several counties of Yunnan Province. After 10 years, there have been significant successes in some places, but there are still many problems with IRM in most parts of Yunnan. Many socioeconomic factors affect the success of IRM. Data were collected from 100 farmers, 6 villages and 3 townships in Tonhai County and from 200 farmers, 1 village and 1 township in Qijin County. All data have been analysed using descriptive statistics, statistical t-tests and benefit-cost analysis.

This study has defined seven important ecological, socioeconomic factors that influence IRM in rural Yunnan.

1. The government needs to provide more assistance in overseeing the organisation of IRM by providing more financial input and training courses for farmers.
2. Although the Chinese Government organises rodent control campaigns on a large scale, including research projects for rodent control, all five levels of government should be involved. If not, each level will deny some of its responsibility for IRM.
3. Farmers need assistance to understand and adopt IRM fully and correctly. Farmers and government officers require more knowledge of the ecological control of rodents.
4. Correct estimations of the benefit/cost ratio for effective IRM must be made so that both the government and the farmers make informed decisions when undertaking IRM.
5. More training courses on IRM are needed, especially for female members of farming families. Females play an important role in the practice of IRM.
6. Inspections for rodent impacts (damage, loss of food, possible diseases) and of the practice and success of IRM need to be done jointly by the government officers and the farmers.
7. The natural enemies of rodents should be protected and there should be careful application of rodenticides to protect the environment.

Rodents in agriculture in the Lao PDR

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Rice accounts for more than 80% of the cultivated land area in the Lao PDR. Rodent problems are mainly associated with rice cultivation. Rainfed lowland rice accounts

for about 70% of the area and 78% of production. Rainfed upland rice accounts for about 25% and 15% of the area and production, respectively.

Smallholder producers in the main rainfed lowland rice growing areas of the Mekong River Valley generally do not rate rodents as a major pest problem and consistently rank rodents very low among potential production constraints. Conventional trapping techniques are generally capable of giving satisfactory control.

In the upland environment, smallholder producers regard rodents as their most important pest, and rank rodents second only to weeds as the overall most important constraint to production. It is also the production constraint over which they have least control. The severity of the problem varies with locality and between seasons. Complete loss of upland rice crops on a localised basis is not unusual. Conventional trapping techniques do not give adequate control in the uplands. Often areas of lowland cultivation in the narrow valleys in the more mountainous regions are also devastated by the movement of rodents from adjacent upland areas. Official policy is to actively discourage the use of rodenticides as a means of rodent control in both the upland and lowland environments. Little is currently known about the species and ecology of rodents in the Lao PDR.

Ecological characteristics and integrated management techniques for *Rattus rattoides*

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In the rice fields of the Pear River Delta, the main pest rodents are *Rattus rattoides* and *Bandicota indica*. Studies on the ecology and management of *Rattus rattoides* have been conducted since 1987. The fluctuations in the reproductive capacity of *Rattus rattoides* between years and in different seasons were studied, as were the population dynamics and rates of recovery of the population after use of chemical pesticides.

The ecological factors affecting *Rattus rattoides* population density were analysed. Several factors, including crop structure, vegetation stage and the height of the ditch banks in the fields directly affected the conditions of habitat and food supply. These factors also greatly affected the spatial distribution of the population in the habitat. When different crops were simultaneously cultivated in the area, pest rodents shifted from one crop to another causing damage.

The frequency of rice damage and the spatial distribution of types of rice damaged by rats were measured. The relationship between the rodent density and rice yield-loss was simulated in a mathematical model and the economic thresholds for *Rattus rattoides* and for multiple-species were calculated.

The sampling techniques for estimating population density of *Rattus rattoides* are presented. The model for forecasting *Rattus rattoides* population numbers was set up using a triple exponential smoothing model combined with a seasonal adjustment model based on the regular seasonal and annual changes in the rat density. The accuracy rate of forecasting was 83%.

Two synergistic rodenticides (chronic rodenticide + synergist) were screened. The dose of chronic rodenticides was markedly decreased if synergistic rodenticides were used. The band-broadcast technique, a high efficiency baiting method for killing rodents, was developed and required coordinated application of acute and chronic rodenticides to reduce the dose in the bait.

The population density of *Rattus rattoides* was managed using integrated management techniques, involving ecological and chemical control. In demonstration tests the highest density of *Rattus rattoides* was reduced from 36% to 9%, and crop damage was decreased from 5–10% to below 0.5%.

A field trial of integrated management of commensal rodents in the residential quarters of the urban area

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A field trial lasting for 2 years was carried out in Tianmen, Hubei to explore methods for management of commensal rodents in residential quarters of urban areas. Three areas were used in the trials: a control area; an area where rodenticides only were applied; and a third area where integrated management including ecological measures was applied. The results show that applying integrated management with ecological measures playing a leading role can achieve a similar or even better effect than using rodenticides alone against commensal rodents. Integrated management not only brings the rodent problem under control, but also reduces or avoids the side-effects of other methods. The side-effects of rodenticides include environmental pollution, accidental poisoning, secondary poisoning, short-term effects, rodenticide tolerance and resistance, and extra consumption of manpower, money and material resources.

The pest characteristics and control of rodents in Tulufan agricultural area

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The ecological habitat characteristics, pests and control of rodents in the Tulufan agricultural area were studied from October 1997 to June 1998. There were six

species of rodents in four habitats in October 1997. The capture rate was 38% (295/650). The major species were *Mus musculus* (31%), *Meriones erythourns* (27%) and *Merionus meridianus* (22%). Other species were *Rattus norvegicus* (18%), *Cricetulus migratorins* (1%) and *Apodemus sylvayicus* (less than 1%). The highest densities of rodents were observed in three habitats: grape cool house (62%), grapery (60%) and furrow (60%), and the major species were two gerbils and *Mus musculus*, the lowest densities were in the residential area (30%).

Migrating activity, home range and characteristics for collecting baits were observed for *M. erythourns*. Using these results the reasons for damage were analysed. In an agricultural area (1300 ha), the effect of 0.005% and 0.01% bromadiolone against rodents was 96.6% and 97.2%, respectively. For 0.1% diphacinone (Na-salt) 94.3% (90–98.8%) mortality was achieved in December. This was the best period of the year for killing rodents in the agricultural area.

Age structure and breeding performance of the rice field rat in West Java

Rahmini and Sudarmaji

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This study was part of a population study of the rice field rat, *Rattus argentiventer*, in rice fields of West Java. This region has a distinct wet season with most of the rainfall occurring from November to May. There are generally two rice crops grown each year, one in the wet season (plant November or December), the other in the dry season (plant April or May). From the 1995 dry season to the 1995–96 wet season, we examined changes in the age structure and the relative breeding performance of different age cohorts of rats.

Rats were obtained from a permanent trap-barrier-system (TBS) which includes multiple live-capture traps. Eye lens weight was used to estimate age, based on a regression formula developed by Japanese researchers working on the rice field rat in West Java in the 1980s. Breeding condition of females was determined at autopsy. The number of embryos, the number of sets of uterine scars, and the size of the uterus were recorded. We also recorded whether females were lactating.

Changes in the age structure of rat populations living in the rice fields were linked closely to the seasonal information on reproductive condition. There were two breeding seasons recorded—both began during the maximum tillering stage of the rice crop and finished (< 10% females breeding) within 2 weeks of harvest. In the fallow period of the dry season (August, September), 1328 rats were captured. The dominant age class was rats 2–3 months old, indicating that there was high recruitment of young rats into the population in the two months after cessation of breeding.

During both the dry and wet season rice crops, rats which were 1–3 months old were absent from the seedling stage through until the early booting stage. This cohort of rats began to enter the population during the panicle initiation stage of the rice crop.

There was marked temporal variation in the sex ratio and breeding performance of different cohorts. For example, during the panicle stage, females aged 5 to 9 months were the dominant cohort. Generally, during the non-breeding season to the early breeding season the males and females were equally present. During the land preparation and transplanting, males aged 8–11 months were the dominant cohort. During early fallow, most of the pregnant females were 2 months old (56%), whereas during the booting stage, most of the pregnant females were 8 months old.

Male rats had scrotal testes throughout the period of this study. Breeding condition of males (as indicated by scrotal testes) peaked during the booting stage of the rice crop, with an average scrotal width of 25.2 mm.

Rodent management and support network in Southeast Asia

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A 4-year project on the management of rodent pests in rice ecosystems will begin in January 1999 in Indonesia, Laos, Malaysia and Vietnam. The project builds on a previous 4-year project, which examined non-chemical control techniques, and the population ecology and habitat use of the rice field rat, *Rattus argentiventer*. The project is funded by the Australian Centre for International Agricultural Research (ACIAR).

The main objectives of the new project are:

1. to develop ecologically-based management of rats at the village level in rice agro-ecosystems;
2. to understand the key factors that limit these rat populations to enable forecasts of years of high rat densities;
3. to investigate species-specific fertility control for rodent pests using oral contraceptive baits; and
4. to foster a dynamic rodent pest network for Asia and elsewhere.

The rodent network will consist primarily of a twice yearly rodent newsletter 'War against Rats' and the 'Rodent Ecology Network' coordinated by CSIRO. The network functions under the umbrella of the International Rice Research Institute (IRRI) IPM network in Asia, coordinated by Dr K.L. Heong.

The rodent network aims to:

- raise the profile of research on rodent management at government levels;
- organise a rodent bibliography on research in Asia;
- develop technique manuals;

- develop a regional approach to rodent pest management;
- establish and apply principles of rodent ecology for management of pest species;
- network through bulletin boards, newsletters and international conferences; and
- tap funds of donor and government agencies for rodent research.

As a first step, CSIRO has established a Rodent Pest Network ‘bulletin board’—an email network that allows anyone on the mailing list to send and receive messages to and from all other members of the network. To subscribe to the Rodent Pest Network bulletin board, simply send an e-mail message to: < MajorDomo@dwe.csiro.au > then write in the body of the text: subscribe rodent-pest-network.

To send a message, update or announcement to the Rodent Pest Network bulletin board, simply send the message to: < rodent-pest-network@dwe.csiro.au >.

If you have any problems, or have any queries about the bulletin board, please email < amanda.lewis@dwe.csiro.au >.

Rice as a trap crop using trap barrier system for controlling the rice field rat (*Rattus argentiventer*) in West Java, Indonesia

Sudarmaji, Jumanta and Rochman

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In Indonesia, the rice field rat, *Rattus argentiventer*, is the most important preharvest pest of rice. We report on a physical method of control which consists of a rectangular fence with multiple-capture traps inserted at its base. Rats are attracted to the traps because the fence surrounds a rice crop that is planted either earlier or later than the surrounding crop. The crop inside the fence is referred to as a ‘trap crop’ and the complete system is called a trap-barrier-system (TBS). In 1996–97, a 1 ha TBS (100 × 100 m) with a rice ‘trap crop’ was erected for three consecutive seasons on a research farm at the Research Institute for Rice in Sukamandi, Subang, West Java. For the three consecutive crops planted from June 1996 to June 1997, the trap crop was planted 4 weeks later, 3 weeks earlier, and 8 weeks earlier, respectively, than the surrounding rice crop. The TBS consisted of 0.7 m wide plastic sheeting supported by bamboo sticks. Twenty multiple-capture live-traps were inserted intermittently at its base. We recorded the number of rats caught each day and the sex of each rat.

During the dry season (June–Sept 1996), when the trap crop was planted late and therefore was growing after the surrounding rice crop had been harvested, 11,488 rats were caught. During the 1996–97 wet season (October–January), the trap crop was planted earlier than the surrounding crop. The number of rats caught per month ranged from 28 to 406. The most rats were caught in December, when the rice trap crop was at the generative stage and the surrounding crop was at the tillering stage. During the 1997 dry season (March–June), the trap crop was an early crop again. The number of rats caught per month ranged from 1241 to 2062. When the trap crop was

transplanted, the surrounding crop land was fallow. When the trap crop was in the generative stage, the surrounding crop was at the tillering stage.

This study indicated that rice as a trap crop within a TBS was attractive to rats, whether it was an early or late trap crop. During the three consecutive rice crops, 26,556 rats were caught. Interestingly, the overall sex ratio was close to unity (1 male to 1.02 females). In West Javan rice fields, rat population densities are generally lower in the wet season than in the dry season. This was reflected in the present study with many more rats caught in each of the dry seasons than the wet season.

Management of rodent pests in the Red River Delta, Vietnam

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In Vietnam, the rodent problem in agricultural crops has escalated in the past 5–10 years. The area of crops with high rat damage has increased from approximately 50 000 ha in 1993 to more than 310 000 ha in 1997. In June 1997, the Vietnamese Ministry for Agriculture and Rural Development classified rodents as one of the three most important problems faced by the agricultural sector.

In August 1996, a collaborative study on the biology and management of rodent pests began in Habac province in the Red River Delta of Vietnam. The Australian Centre for International Agricultural Research (ACIAR) supported the study. There are two rice crops grown per year in the delta: a wet season crop and a dry season crop. From October 1996 to April 1998, we measured changes in the dynamics, breeding performance, habitat use, and species composition of the rodent populations. We also examined a new generation trap-barrier-system (TBS) that had been successfully trialed in Indonesia and Malaysia.

The major rodent species in the rice-ecosystem were the rice field rat, *Rattus argentiventer*, (56%) and the lesser rice field rat, *Rattus losea*, (20%). Rats were most abundant from the booting stage of the rice crop to a month after harvest, and during the ripening stage of soybean crops. Females began breeding at the maximum tillering to booting stages of the rice crop, irrespective of whether it was the wet or dry season. Males were in breeding condition throughout each of the cropping seasons.

The rats that entered the multiple-capture traps of the TBS were predominantly *R. argentiventer* (81.3%), with the highest trap success occurring at the booting stage of rice (51% of rats were caught then). The TBS provided a halo of protection to the surrounding crop; rice yields were higher closer to the TBS. The reduction in rice yield was 10.7% on the untreated site and was 0, 3.7, 4.3 and 8.1% at 0, 50, 100 and 200 m from the TBS, respectively.

The TBS approach is just one of a number of actions that may contribute to a significant reduction in losses caused by rats. Other possible activities include synchronous planting of crops; reduction in width of levee banks; control of grasses and weeds along banks, upland areas and village gardens; removal of rice stubble as soon as practicable; and well targeted use of rodenticides. The challenge is to critically evaluate whether these ecologically-based management actions significantly reduce the impact of rodent pests at the village level.

The primary application of classification of types of rodent damage for regional rodent control

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From 1988 to 1993, the rodent community on about 110 000 km² in a semi-arid region of Inner Mongolia was investigated using traps (131 109 trap nights on 251 sites). The raw data matrix was composed from information about the species composition and site numbers. A cluster method using statistical software (SAS system) was used to identify communities. The rodent communities were divided into nine types, depending on the characteristics of topography and vegetation in the region. In accordance with characteristics of distribution and structure of the communities, the semi-arid zone was divided into five major rodent damage regions and seven rodent communities.

Type I: rodent damage in desert–steppe area

- (1) *Phodopus roborovskii*, *Dipus sagitta*,
- (2) *Allcataga bullata*, *Citellus erythrogitta*

Type II: rodent damage in steppe–desert area

- (3) *A. bullata*, *D. sagitta*

Type III: rodent damage in sand area

- (4) *P. roborovskii*, *D. sagitta*, *Meriones unguiculatus*

Type IV: rodent damage in dry farmland on the north parts of Yinsan mountains area

- (5) *M. unguiculatus*, *P. roborovskii*
- (6) *C. dauricus*

Type V: rodent damage in secondary and artificial forest on the middle parts of Yinsan mountains area

- (7) *Clethrionomys rufocanus*, *Apodemus speciosus*.

A rodent pest control strategy for the semi-arid zone was suggested using simplified information about classification of the type of rodent damage in the semi-arid zone.

Symposium D

Control Techniques (Chemical Control and Resistance; Physical Control, etc.)

PLENARY LECTURE

Current status of rodent management in the United States

Dale Nolte

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An overview is given of the status of rodent management in the United States. Though new technical approaches (e.g. immunosterilisation) may be on the horizon, recent changes probably having the greatest impact on rodent management are not evolving methods. Rather, they are public attitudes, registration requirements and problem perceptions. Increasing concerns for animal welfare and the environment make it necessary to reassess approaches, and to ascertain that the end does justify the means. Registration requirements have rendered it uneconomical to maintain some tools and it is becoming more difficult to register new ones. Effort is becoming increasingly directed towards solving problems rather than reducing populations of depredating species.

Rodent management generally reflects efforts to reduce problems inflicted by rodents. However, efforts to protect threatened or endangered species are also increasing. Twenty-one rodent species are listed as endangered by the U.S. Fish and Wildlife Service as of 31 August 1998. Another two species are listed as threatened. Management to protect these species is primarily focused on protecting habitat or at least limiting human activities in areas where they are known to occur. For example, timber harvest restrictions have been proposed near areas occupied by the Point Arena mountain beaver. Specific efforts to directly manage species that prey on endangered rodents or compete with rodents for resources are far less common.

Four broad categories of problems targeted for rodent management are conservation, human health, commensal, and agriculture. Introduced rodents threaten many wild-life species. There are increasing efforts to manage rodents to enhance the viability of other species, particularly those species at risk of extinction. Rodents can and do affect human health. Rodent management to reduce risk of disease has long been practised. Problems with commensal rodents continue, including sanitary concerns, structural damage and utility disruption. Agriculture losses can be substantial. The type of damage reflects the cropping system and the particular rodent species.

Multiple tools or approaches are available to alleviate problems induced by rodents. The efficacy of techniques to reduce problems varies and is dependent on the technique, the situation and the applicator. Ecological and cultural approaches include

improving sanitary conditions, reducing habitat, providing alternative foods, or rotating crops. Water flow devices have reduced some flooding problems caused by beavers. An assortment of barriers is available to restrict access by rodents. Few chemical repellents are currently available to deter rodents and the efficacy of those available is questionable. Ultrasound techniques basically do not work because of sound shadows, minimum distance carried and rapid habituation by animals. Animals avoid electrical shock, but few applicable methods have been developed for operational use. Textural repellents have demonstrated potential for some rodents under selected conditions. Traps are commonly used to eliminate commensal rodents and in field conditions where toxins are not feasible. Efforts are being made to develop sterilants for rodents, but none are currently available. Registration issues are limiting the number of toxicants available for application. This help to maintain a safe and clean environment, but increasing data requirements and costs of generating these data have made it uneconomical for many private and public registrants to maintain pesticides. Emphasis is focused on maintaining existing toxicants. Few or no research efforts are directed towards developing new products.

Integrated pest management (IPM) consists of using a mixture of approaches and tools to address various aspects of existing or potential problems. Multiple tools may be incorporated simultaneously into an IPM, or different tools may be applied depending on population levels, problem intensity or specific behaviours.

ORAL PRESENTATIONS

The management of rodent pests of agriculture—20 years on from the Paris OECD/FAO/WHO Expert Consultation

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Exactly 20 years ago the world's rodent control specialists were gathered in Paris by the Organization for Economic Co-operation and Development, the Food and Agriculture Organization and the World Health Organization to determine what were the major rodent pests of the world's agriculture and what should be done about them. Their opinion was that six rodent pest problems existed of global significance which resulted in serious losses of food crops grown by smallholders, mainly in countries of the tropics and sub-tropics. These problems were those presented by *Rattus argentiventer* in Southeast Asia, *Bandicota bengalensis* in South Asia, *Praomys natalensis/Arvicanthis niloticus* in sub-Saharan Africa, *Sigmodon hispidus* in Latin America, *Meriones* spp. in North Africa and the Middle East and *Rattus* spp. among the islands of the Pacific Ocean. Subsequently, internationally-funded projects were strengthened on four continents to develop appropriate control measures. As a result of these initiatives it may be said that cost-effective methods, mostly based on the application of anticoagulant rodenticides, are now at hand to control rodent pests in most of these situations. But although these proven techniques are available, rodent pests still devastate large areas of the world's agriculture every year and deny food to hungry

people in many countries. This paper describes the evolution of the strategies currently used for protecting growing crops from attack by rodent pests and examines the reasons for success and failure when they are applied.

Development and field evaluation of a blood clotting response resistance test with rats using coumatetralyl

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Rat control measures may fail to be completely successful for different reasons. In some areas a decrease in the susceptibility to anticoagulant rodenticides has been observed. To test the susceptibility of wild rats, blood clotting response (BCR) tests have been developed for most of the commonly used anticoagulants. BCR tests allow a quick estimation of the susceptibility of individual rats to different compounds. However, the level of resistance detected using these tests does not necessarily reflect control efficiency of field treatments with the respective compound, as appropriate investigations have not yet been conducted. In this study, baseline data for coumatetralyl were collected to establish a BCR test. In a first approach a 96-hour test was designed according to testing results with six doses between 8 mg and 15 mg/kg bodyweight (bw), the discriminating dose calculated using probit analysis being 13 mg/kg bw. However, results of field treatments on farms in the Münsterland area showed no correlation to BCR prognosis. In most of the populations sampled less than 10% of the individuals were classified susceptible, whereas the mean efficacy of field treatments was 65%.

A 24-hour test, developed in a second approach, was found to be more satisfactory in 1) providing quicker results and 2) forecasting field efficacy more accurately. Of 195 Wistar-derived albino rats tested at doses between 5 and 12 mg/kg bw, all but one individual (at the lowest dose) responded, showing prolonged clotting times; <12.5% blood clotting activity (BCA) after 24 hours. 100 wild rats of a warfarin- and coumatetralyl-susceptible outbred laboratory strain were BCR-tested with coumatetralyl dosages ranging from 0.5 to 10.0 mg/kg. BCA of all individuals was below 12.5% for all dosages 24 hours after application. In contrast, 42% of 166 wild caught rats from the Münsterland area had returned to clotting times above 12.5% after 24 hours. According to these results 7 mg/kg bw was determined to be the appropriate discriminating dose.

Most of the anticoagulants are characterised by a lethal feeding period (LFP₉₉), which for coumatetralyl is supposed to be 4 days at most. For comparison, 40 wild caught rats, 20 classified susceptible and 20 resistant according to the BCR test, were given a 4-day no-choice feeding test on normal field strength coumatetralyl. All individuals (10 males and 10 females) determined to be susceptible by BCR testing died during or shortly after the feeding test. But also 1 of 10 females and 4 of 10 males

died, though they had been tested resistant. Work is in progress to better define the LFP₉₉. Preliminary findings suggest that this value could be as little as 2–3 days for susceptible rats. In any case, males seem to be more susceptible than females according to both BCR and feeding tests.

Results of this study suggest that a BCR test, though allowing a distinct discrimination between susceptible and resistant individuals in the laboratory, may not adequately forecast the efficacy of control operations in the field. Available BCR tests should be reanalysed and probably adjusted in relation to field results to improve their value in reliably predicting field efficacy.

Resistance test methodologies—a novel test procedure for the potent second-generation anticoagulants

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Resistance to the first-generation anticoagulants was first discovered in the Norway rat (*Rattus norvegicus*) in 1958. However, further reports, both in this and other species, from Europe, the USA, South America and Japan, generated major concerns over the future of the early anticoagulant rodenticides. Methods were quickly developed to identify rodents resistant to warfarin, so that their spread could be monitored and the practical importance of warfarin resistance determined. Discriminating doses used in resistance checking tests were based either on lethal feeding periods fatal to 99% of a susceptible population (the LFP test), or on doses of anticoagulant that caused prolonged clotting times in 99% of a susceptible population (the blood clotting response [BCR] resistance test). These tests were robust because of the high tolerance to warfarin conferred by the resistance genes.

In the 1970s, the second-generation anticoagulants were introduced to control rodents resistant to the first-generation compounds, although subsequent localised reports of resistance to some of these compounds have been reported. The adoption of LFP and BCR test methodologies for the second-generation anticoagulants has not been straightforward. In the case of the LFP test, it is difficult with the most potent compounds to establish a statistically valid dose-response line to allow a discriminating dose to be derived. With the BCR tests, the outcome of checking tests can be difficult to interpret in terms of their ability to predict actual treatment failures.

This paper considers the advantages and disadvantages of existing laboratory methods for resistance testing, and proposes a novel test procedure for detecting resistance to the potent second-generation anticoagulants. This test procedure is designed to provide objective data that is more readily related to the field situation, giving better insight into the likely outcome of treatments at resistance foci.

Warfarin resistance in the rice field rat, *Rattus argentiventer*

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Warfarin was the most commonly used anticoagulant rodenticide since the 1940s and resistance to warfarin in the brown rat, *Rattus norvegicus* Berk., was first discovered in Scotland in 1958. In Peninsular Malaysia, warfarin-resistant populations of feral house rats, *Rattus rattus diardii* (Jentink), were first reported in oil palm and cocoa estates in 1980. Subsequently, very high tolerance to coumatetralyl was found in a population of *Rattus tiomanicus* Miller in 1983. This paper reports the development and detection of warfarin-resistance in the rice field rat, *Rattus argentiventer* (Robinson & Kloss), in Malaysia. The base-line susceptibility of a laboratory colony of warfarin-naive *R. argentiventer* was established in 'no-choice' feeding tests with 0.05% warfarin. During tests, the rats (20 males and 20 females for each feeding period) were given a sole diet containing 0.05% warfarin for a fixed number of days. Bait consumption and mortality were recorded and dead rats were autopsied for evidence of anticoagulant poisoning. Rats that remained alive at the end of the various test periods were further observed for 30 days. The feeding period/mortality data were analysed by probit analysis. From time to time, rat samples were obtained from an area treated with 0.05% warfarin since 1974 for screening against 0.05% warfarin. In 1994 a sample of 38 rats, collected from the warfarin-treated area, was fed with a sole diet of 0.05% warfarin for 14 days. Bait consumption and mortality of the rats were recorded. Survivors were observed for 30 days after tests, and dead rats were autopsied for evidence of anticoagulant poisoning. The results of the feeding tests were then compared with warfarin-naive rats. Base-line susceptibility studies with 0.05% warfarin against warfarin-naive rats indicated a median feeding period (LFP_{50}) of 2.7 days and a LFP_{99} of 12 days. The lowest susceptible dose in males was 33.0 mg/kg and in the females was 20.8 mg/kg. In the sample of 38 wild-caught rats exposed to a sole diet of 0.05% warfarin for 14 days, five rats (three males and two females) survived the test. The highest dose ingested by a wild male survivor was 219.6 mg/kg and for the wild females was 263.9 mg/kg. The proportion of wild males in the sample surviving the 14-day test was 17%, and was 10% in wild females. The expected survival rate of a normal population of *R. argentiventer* was 1% when subjected to a feeding period of 12 days with 0.05% warfarin. Under the more stringent 14-day test with 0.05% warfarin, 13.5% of the rats from the field population survived and this indicated a 13.5-fold increase in the survival rate of rats in the treated wild population. The five wild rats that survived the above test were considered resistant to the anticoagulant rodenticide warfarin.

Impact of rodents on reforestation in the United States: problems and management

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Rodents foraging on young tree seedlings often hinder reforestation efforts. Efforts to establish tree seedlings on sites infested with rodents can be futile unless measures to reduce damage are implemented. An overview of the biology and behaviour, damage characteristics, and management approaches to reduce problems is provided for mountain beaver (*Aplodontia rufa*), pocket gopher (*Thomomys* spp.), porcupine (*Erethizon dorsatum*), vole (*Microtus* spp.) and beaver (*Castor canadensis*). Methods to maintain water flow and reduce flooding caused by beaver are described. Impacts on forest resources by other species, such as squirrels (*Sciurus* spp., *Tamiasciurus* spp.), mice (*Peromyscus* spp.) and woodrats (*Neotoma* spp.) are also discussed.

Secondary poisoning risks associated with broad-scale field use of brodifacoum in New Zealand

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The broad-scale field use of brodifacoum baits to control rats and possums has increased in recent years. This has raised concerns about secondary and even tertiary poisoning of humans resulting from the transfer of this toxicant through the food-chain. We have determined experimentally the concentrations of brodifacoum in muscle and liver of captive pigs after primary and secondary poisoning. This approach is complemented by the measurement of brodifacoum residues in feral game species (pigs, deer and goats) and in introduced and native birds and invertebrates. Brodifacoum concentrations exceeding 1 mg/kg are being found in game species and trace amounts have been found in kiwi.

Clearly there is a risk of exposure to brodifacoum and perhaps even toxicity for humans consuming feral pigs, which could be compounded by pigs eating both bait (primary poisoning) and poisoned carcasses (secondary poisoning). The increasing incidence of brodifacoum residues in birds, including treasured native species, and the unknown effects of sublethal contamination are heightening concerns regarding the toxicology of brodifacoum in the environment.

Rat control: legislation and administration in Denmark

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Danish rat control has been legislated since the beginning of the century. The aim of the law and its statutory order is to control rat populations effectively so their presence will not give rise to unhygienic conditions, health problems or other nuisances

to the public. The control has to be carried out with maximum safety for human beings, domestic animals and pets. The strategy of rat control has changed from eradication to control but some old principles from the early days are still valid:

- rat control must be carried out on large, geographically connected areas; and
- rat control must be taken care of by the public

Organising rat control in detail may be done in a number of ways. This study focuses on Danish legislation and how rat control is being organised. Local councils in each municipality are responsible for conducting and administering rat control. Each year they have to submit written information to the Danish Environmental Protection Agency (DEPA) on how rat control is carried out: number of notifications received about rats; houses visited; name of contractor; amount of contract; supplier of anticoagulants; name of anticoagulants used; number of blocs used for sewer control; method of finance etc. Official notifications on rats per year are around 100 000.

Local councils can contract private companies to control rats; this is so in 84% of cases. There are about 50 private companies authorised in Denmark. The authorisation is not granted to the company itself but is a personal license for one or more of the employees. The authorisation is obtained if the applicant attends a course on rat control and passes a final test issued by the DEPA. Since 1983, 395 persons have attended the 17 courses. Of these, 196 were from local administrations within municipalities and 153 were from private pest control companies. However, the majority of pest controllers within the private sector are still unauthorised. In five major companies only 24% of staff involved in rat control are authorised.

Denmark was among the first countries in Europe to discover resistance towards anticoagulants in Norway rats. Since then resistance has become a serious but still not insurmountable problem for rat control. Resistance has been detected in perhaps three of the six anticoagulants used on the Danish market. The Danish Pest Infestation Laboratory carefully monitors the development of resistance throughout the country. The results are forwarded to pest controllers, giving them an up-to-date view of the local situation. The pattern is clear. Resistance develops faster for each new anticoagulant introduced and spreads rapidly across the country. Therefore, it is of vital importance that unauthorised persons using stronger anticoagulants than necessary do not provoke resistance among rats. Consequently, the DEPA has launched a new strategy. According to the statutory order on rat control only authorised persons or their employees are allowed to use anticoagulants. The DEPA is responsible for monitoring this order. Two advisers are employed to provide both supervision and enforcement. Transgressors risk being charged both of violating the law and having the municipality carry out control measures at their expense. The administration of rat control is financed in two ways. The local council either applies a local tax or levies a tax indexed on the value of real estate. The total budget for rat control in Denmark is about 50 million DKK, or 10 DKK.(app. US\$1.50) per person.

The Danish model on rat control focuses on the role of local authorities with a characteristic centralised governmental control. Other countries around the world may chose to

do rat control differently and in fact has done so. A table showing the differences and/or similarities of a number of countries in and outside Europe is presented and discussed.

Cinnamamide: a repellent for commensal and field rodents?

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Public concern for the environment and animal welfare has created a need to consider non-lethal, environmentally-sensitive methods of controlling rodent pests. Chemical repellents can provide an alternative to pesticide-based control techniques but, until recently, the effect of many such chemicals was often short-lived, or the compound was toxic or odorous to man and consequently not widely used. This paper provides an overview of the potential uses for these chemicals in rodent population management and investigates the potential of cinnamamide, a derivative of naturally-occurring plant secondary compounds, as a rodent repellent. Cinnamamide has been shown to deter a broad range of pests including bird (e.g. feral pigeons; *Columba livia*), mammals (e.g. Norway rats; *Rattus norvegicus*) and invertebrates (e.g. field slugs; *Deroceras reticulatum*). Its potential was also evaluated against house mice (*Mus domesticus*) and wood mice (*Apodemus sylvaticus*), both of which pose problems that could be reduced by using a repellent as a feeding deterrent. Both species were presented with cinnamamide-treated food. Consumption of the treated food was maintained at control levels for a short period (3 hours) before a significant decline was observed ($p < 0.05$). Consumption of treated food by the house mice remained depressed for the duration of the trial. In contrast, the wood mice rapidly habituated to the presence of cinnamamide. The different responses of the two species may reflect their respective feeding ecologies. Repellents are either innately aversive in terms of their taste/odour or they give rise to a learned aversion, i.e. the individual associates the taste of the compound or another cue with its post-ingestional effects and will avoid that cue in future encounters. The delayed response observed with the mice is indicative of a learned aversion and is in sharp contrast to cinnamamide's effect on birds which find it to be immediately aversive. The efficacy of cinnamamide as a learned aversion agent was examined by pairing the chemical with a novel flavour (saccharin) and subsequently testing for the avoidance of the flavour with house mice. The results showed that mice treated with a single dose of cinnamamide developed a complete and persistent aversion to the novel flavour over the entire trial (64 days). Our results show that cinnamamide has the potential for use against the commensal rodent (*Mus domesticus*) in some situations (e.g. food production areas and in conservation areas) as an alternative to lethal control methods.

Studies on resistance to anticoagulant rodenticides in China

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Studies on resistance to anticoagulant rodenticides began in China in the late 1970s. In 1980, several institutes carried out preliminary tests on the susceptibility of commensal

rodent species to warfarin using the WHO testing procedure. Given the widespread use of anticoagulant rodenticides in China, a National Collaborating Group on Rodent Resistance Surveillance (NCCRRS) was established in 1985. Its activities were carried out under the leadership of the Vector Biology and Control Society of China.

Using baseline results for susceptibility to warfarin and reference to the international literature, criteria for defining resistance were developed for individuals and populations of three commensal rodent species caught in representative areas of China. Individual *Rattus norvegicus* were considered anticoagulant resistant if they survived a 6-day no-choice feeding of 0.005% warfarin bait while consuming a minimum 12 mg active ingredient/kg. Individual *R. flavipectus* and *Mus musculus* were considered anticoagulant resistant if they survived a 9-day and an 11-day no-choice feeding of 0.05% warfarin bait while consuming a minimum 143 mg active ingredient/kg and 338 mg active ingredient/kg, respectively. Populations of any of these species were considered resistant if 15% or more individuals ($n > 20$) survived the above test protocol.

Anticoagulant resistance in the three commensal rodents was investigated in 39 localities of 18 provincial, city and autonomous regions where anticoagulant rodenticides had been applied for more than 4 years. Of 1604 individuals tested, 72 showed resistance (*R. norvegicus*, 33/837; *R. flavipectus*, 30/524; *M. musculus*, 9/243). With the exception of *R. norvegicus* from Shanghai, no resistant populations were found for the three species examined. There was also no resistance observed in the areas where the rodenticides had been used for less than 6 years. In areas where the anticoagulants had been used for 8 years, there was no significant difference ($p > 0.5$) in the susceptibility parameters for *R. norvegicus* and *R. flavipectus*, although the dose-response curves for the susceptible rats versus non-susceptible rats were significantly different ($p < 0.01$). These results indicate that the development of anticoagulant resistance in the rats is similar to the development of pesticide resistance in pests.

Second generation anticoagulant rodenticides (SGAR) were developed after the discovery of resistance to first generation anticoagulants (FGAR). In China, because FGAR have not been used widely in all areas, resistance to them should be demonstrated before SGAR are used. NCCRRS recommends that active surveillance and understanding of resistance should guide reasonable use of anticoagulant rodenticides in China to the benefit of society.

Field trials with the anticoagulant 'Stratagem' against rodents in special environments

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The aim of the trials was to demonstrate the efficacy of 'Stratagem' for control of rodents in different environments. 'Stratagem', provided by the Cyanamid company, is a new-generation anticoagulant rodenticide with good palatability.

The trials were divided into three stages. For the first stage, 'Stratagem' baits, 'Stratagem' bait blocks and cut wheat baits containing 0.005% flocoumafen, were used at an average rate of 10 g/15 m². Responses were determined using tracking tiles. The rates of population decline were 88% at the hospital, 91% at the hotel and 87% at the chicken farm.

For the second stage, 'Stratagem' powder with 0.1% flocoumafen was mixed in a ratio 19:1 with breadcrumbs, maize powder, or carrot pieces to control remaining rodents. The rates of population decline were up to 99% at the hospital and 98% at the hotel.

The third stage used environmental techniques, especially management of food availability and implementation of rodent proofing. The rates of population decline increased to 100% at the hospital and 99% at the hotel. Four months later, the rodent population densities had increased to 0.3% at the hospital, 0.9% at the hotel and 13.9% at the chicken farm. At this time the rodent population at the chicken farm was higher possibly due to the lack of second and third-stage control measures.

POSTER PRESENTATIONS

Management of mouse plagues in Australia using ecologically based pest management

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Plagues of house mice (*Mus domesticus*) occur in the grain-growing regions of southern and eastern Australia, causing up to \$100 million in damage to crops. A mouse plague occurs somewhere in Australia every four years. The management of mouse plagues once they have erupted (densities >1000 mice/ha), generally relies on the use of broad-scale acute rodenticides such as strychnine or zinc phosphide. Recent research has examined the effect of modifying habitats on farms to reduce the food supply and shelter available to mice. If mouse populations could be managed before the build-up in density, less damage would occur on the farm. In order to determine what sort of management actions were required, an advisory panel consisting of researchers, farmers and industry personnel was formed. The panel devised a list of actions that farmers could undertake at different stages of the crop over different densities of mouse populations. Research over the past 16 years has provided a strong ecological understanding of mouse plagues, and farmers provided a good understanding of whether the actions could fit into their farming routines and could be cost-effective. These actions were tested in a replicated field experiment in the winter-cereal-growing region of Victoria, Australia. Results showed that managing plant growth along the edges of crops in early spring (onset of breeding of mice) reduced the number of mice present in late summer. Putting sheep on to graze immediately after harvest reduced the amount of grain remaining on the ground (spilt grain is a high quality food source that can maintain breeding).

In a new study, a set of recommendations will be developed for an irrigated, summer-cropping area in southern New South Wales. An advisory panel will consist of researchers, farmers and industry representatives. Every 6–8 weeks we will monitor the response of mouse populations to the imposed management actions. Just before harvest of both the summer and winter crops, we will assess the losses caused by mice. Also, we will examine the potential of simple monitoring systems for estimating the size of mouse populations to aid farmers in their decisions to undertake early management actions.

Efficacy and value of flocoumafen (STORM®), a second generation anticoagulant, in public health and agricultural rodent pest control

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Every year rodents create grave public health concerns, cause untold property damage, and consume and contaminate vast amounts of foodstuffs throughout the world. Trials conducted worldwide have demonstrated the efficacy of flocoumafen against a variety of rodent pests in commercial, domestic, and agricultural premises and in agricultural crops. The results of flocoumafen treatments demonstrate significant reductions not only in rodent populations but also in crop damage and labour costs compared with local practices.

Palatability and toxicity tests with a systemic insecticide in a rodenticide bait for rat and flea control

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Vector/reservoir control in plague endemic areas must target rodents as well as their flea ectoparasites. Traditionally, insecticides are dusted before the application of rodenticides, or an insecticidal powder is applied in a bait box where rodents enter to reach the rodenticide. Both methods have their logistic problems. We investigated the possible use of fipronil as a systemic insecticide to be mixed in an anticoagulant rodenticide bait.

Four different concentrations of fipronil (0.05%, 0.005%, 0.0005%, with acetone as a solvent, and 0.05% with propylen glycol as a solvent) and two control solutions (solvents only) were combined with a rodenticide bait consisting of crushed organic wheat and 0.005% bromadiolone. Each concentration was offered together with an unpoisoned alternative bait (crushed organic wheat) to 10 singly caged *Rattus rattus*. One hundred rat fleas *Xenopsylla cheopis* were placed in each rat cage one day later. Consumption of both choice baits was monitored daily for four days, after which the rats received unpoisoned standard food. Fleas were removed after six days and kept in a glass tube with sand; flea mortality was checked 24 and 48 hours later. Rodents were observed for 3 more weeks and rodent mortality was checked. All dead rats were autopsied for signs of anticoagulant poisoning.

Bait consumption was relatively low and an unsatisfactory rat mortality of around only 50% was obtained in all tests. The palatability of the bait, however, was not affected by the fipronil concentration although the solvents may have an effect. Flea mortality after 48 hours reached 100% at the highest fipronil concentrations and was still above 95% at the lowest concentration; in the control tests, the natural mortality was below 70%. In conclusion, fipronil has no bad effects on rodent bait palatability and is effective as a systemic insecticide to kill fleas. The bait base, however, has to be more attractive to roof rats in order to be useful in practice.

Control of rodents to alleviate poverty in the Loess plateau of China

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Luliang is located in the centre of the western Loess Plateau. The plateau has a total area of 21 095 km², covering 13 counties and has a continental climate. With 760 000 families, it has a population of 3.4 million and, being one of the poorest districts, is supported financially by the State Council to reduce poverty.

In 1993 a study found there were 5 families, 3 sub-families and 16 species of rodents. There were roughly 20 million rodents in this region (about 10 million in households and 10 million in the field) or an average of 16.8 rodents/ha. Annual grain loss due to rodents reaches 180×10^4 kg. Furthermore, the rodents also spread more than 30 diseases. It is essential to address rodent problems in this region. In 1993, Shanxi Academy of Agricultural Science put rodent control as a priority poverty alleviation project and the government of Luliang took rodent control as an important way to guarantee grain harvest, help farmers overcome poverty and improve their health. Through coordination between the government, academy and farmers, the following studies were carried out: (1) monitoring and forecasting of the dynamics of rodent damage; (2) establishing economic thresholds for different environments; (3) developing regional rodent control measures; (4) establishing a complete set of comprehensive controlling techniques; and (5) developing techniques and strategies for sustainable management. Up to 1997, it was calculated that rodent control covered 0.5 million ha of farming land, killing 100 million rodents, saving about 920 000 t of grain from damage and avoiding economic losses of 760 million Yuan. About 11 million Yuan was invested to do the work and the benefit-cost ratio was 71:1. This rodent control action achieved good economic, social and ecological benefits.

Effectiveness of Diphacinone and Silmine G on *Arvicanthis niloticus*

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In Soudano-Sahelian West Africa, even if there exist some local practices for rodent pest control in certain countries, such as Mali, rodent pest control is generally conducted by chemical means. Anticoagulants, which kill animals remote from the poison source, are generally used because rodents quickly establish a relation between consumption of poisoned food and the death of their congeners. Nevertheless, the risk of development of resistance to anticoagulants may be important. This risk is linked with mobility of rodent populations (it is higher when they are mobile than sedentary), and with the effectiveness of the products. We present here the results of a study on toxicity of Diphacinone and Silmine G on *Arvicanthis niloticus*.

Diphacinone test: 40 animals were separated into groups of 10 (5 males and 5 females). Their usual food was withdrawn and replaced by poisoned food (10 g with active matter 0.005%). The duration of poisoning varied from 1 to 4 days for four respective groups (group 1 to group 4). The unconsumed poison food was removed each day, weighed and replaced by a new amount of poisoned food.

Silmine g test: 36 animals were separated into 3 groups of 12 individuals (6 males and 6 females) and each group received a single amount of poisoned food (2.5%: group 1; 5%: group 2; 10% group 3). The results obtained showed that Diphacinone was more effective in females than in males (95% versus 90% of mortality). It appeared that weight loss was 2.2 times more important in females than in males. In both females and males, the duration of survival increased with the duration of poisoning between 1 and 3 days; after 3 days, the duration of survival had stabilised. It thus seems that the resistance of the animals to Diphacinone increased according to the exposure time during the first three days of poisoning. Silmine G, was less effective (67% of mortality in females versus 50% of mortality in males).

Location of food source in *Mastomys natalensis*, Muridae, Rodentia

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Mastomys natalensis (Smith 1834) is a murid field rodent which is a serious crop pest in eastern and southern Africa. At planting, the rodent systematically retrieves sown seeds of cereals. The search and retrieval of seeds from the ground appears not to be random, because rodents can locate newly planted maize in the ground. Investigated cues were odour from the seed, and landmarks of the field. In the landmarks experiment, seed take by rodents from seed points with soil marks was compared to that from points without marks. In the odour experiment, I compared seed take between dry seeds and water-soaked seeds; and dry seeds to alcohol-soaked seeds.

The highest seed removal was observed on water-soaked seeds planted in dry soil. No seed take was observed from alcohol-soaked seeds, and no significant difference in seed take was observed between seed points with marks and those without. It appears the rodents use odour to locate seed. Further studies are required to identify the chemical nature and source of the smell. The goal of the study is to develop ways of masking the odour from the seed to that rodents fail to locate it.

Species discrimination in interspecific hybrids of two dwarf hamster species supports the odour image hypothesis

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Discrimination and preference of conspecifics or their chemosignals are well documented as mechanisms for ethological isolation in many rodents. The question arises as to how animals make use of the odours or animals they meet. We suggest two hypotheses: 1) matching mechanism; an animal matches step-by-step the information about the species, sex, and finally about the reproductive state and then will react according the information received; 2) 'odour image' hypothesis; when an animal analyses another animal or its chemosignals it perceives the whole image that may represent a female or a male of its own species (to be more precise of the 'learned' or 'experienced' species). Interspecific hybrids are useful natural models to study the role of an early experience for forming species attachment and to test the proposed hypotheses because during postnatal ontogeny they are exposed to adults of different species. Previously we have found that males of the two closely related hamster species (*Phodopus sungorus* ('S')) and *P. campbelli* ('C')) exhibit a strong preference for conspecific males and females and their chemosignals. Cross fostering leads to a reversal of the species-specific preference. For the present study the following hybrids were used: C male × S female (F1D), and S male × C female, (F1R). In preference choice tests hybrid males were allowed to investigate either two anaesthetised pure-bred animals of the same sex but from different species, or their urines (e.g. S male versus C male, and S female versus C female). Based on matching mechanism, we expected that hybrid males would not show any preference. According to the 'odour image' hypothesis, we suggested that hybrids would prefer the male of the paternal species and the female of the maternal species. The results revealed that F1D and F1R hybrid males prefer the male and urine of the male of the paternal species and the female and urine of the maternal species. These results are in agreement with the 'odour image' hypothesis. We suggest that during early postnatal life juveniles learn the whole set of characteristics of their parents and based on them form an 'odour image' of the future social partner.

Impact of rodents versus insects on food products stored in Mossi (Burkina Faso) and Bambara (Mali) regions

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Except in a few cases, damage by rodents has only very seldom been quantified in Soudano-Sahelian West Africa. In order to obtain data in this field, we sought to quantify rodent damage in attics in Mali and Burkina-Faso. In each of the two selected areas (Sapogo, about 80 km from Ouagadougou in Burkina Faso; Djoliba about 50 km from Bamako in Mali), a study was carried out in 8 attics (4 attics in bush and 4 attics in villages) in February and August. In each attic, boxes were used in order to distinguish damage caused by insects from those caused by rodents. These boxes comprised 4 compartments, each contained a different food product cultivated in the two study areas (groundnut, millet, red sorghum and white sorghum). A first type of box was manufactured with openings of 5 × 5 cm, allowing access by both rodents and insects. A second type of box was manufactured with openings of 5 × 5 cm sealed by a fine netting, allowing access to insects only. The third type of box was manufactured with openings sealed by a very fine netting in order to estimate the effect of humidity on food weight. At the end of this study, captures were carried out in order to identify rodent species which caused damage.

The results obtained enable us to analyse the importance of the impact of rodents, compared with that of insects, in the two study regions. We can also consider damage according to the types of grains, the place of storage (bush or village), and the seasons. These results allow us to make some proposals concerning storage of food products in the Soudano-Sahelian region.

Rodent management in rice fields of Thailand

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Rice (*Oryza sativa* L.) is the most important economic crop in Thailand. Rodents formerly caused serious damage to rice crops. The damage assessment performed by the Agricultural Zoology Research Group (AZRG), Division of Entomology and Zoology, Department of Agriculture in 1976–77 revealed that, in all parts of Thailand, on average 6.9% of rice was damaged. During 1980–1990 investigation focused on rodent management in rice. It was a time when the Thai–German Rodent Control Project was set up to develop a rodent control strategy in rice. The objective of this paper is to provide an overview of investigations on rodent management in rice fields of Thailand such as investigation on important species of rodents, seasonal variation of rodent density, crop loss assessment and efficacy of rodenticides both in laboratory and in rice fields. The results of these investigations were integrated in rodent control strategies implemented of communication system to farmers. Since that time

damage in rice has dropped to 1.5% on average of all regions of Thailand. This assessment was performed by AZRG during 1990–1993. Moreover, a primary investigation on potential use of the protozoan *Sarcocystis singaporensis* as a biological control agent for biological control of rodents in rice fields will be included.

Studies of integrated rodent control in the broken Loess plateau gully region

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A regional integrated management system to control rodent pests was ecologically assessed in the broken Loess plateau gully region.

According to the frequency of occurrence of the rodents at different times and places, different specified management practices were used. Key techniques of the system included the following.

1. Selection of the chemical rodenticide, improvement of baiting techniques and of the application methods of the chemicals involved.
2. Rationalised use of the trap apparatus to catch the remaining rodents but without damage to the surrounding growing plants.
3. Utilisation of agricultural methods to control the number of rodents.
4. Environmental management and ecological measures to control the damage caused by the rodents is stressed.
5. Protection and utilisation of the natural enemies of the rodents and development of regulation through ecological links.
6. The economic threshold of the main rodent species was studied in order to increase the scientific basis for making policy decisions about rodent control.

Initially, chemical control and capture methods reduced the population density of rodents. Later, methods such as agricultural methods, ecological engineering and natural enemies were used to prevent the rodent density from recovering. This management system was carried out between 1992–1995 in a 13 km² area of Xixian, Shanxi Province and achieved good results.

An introduction to the anticoagulant rodenticide, diphacinone sodium salt

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Dalian Chemical Experimental Factory (PRC) is the only factory in China producing the anticoagulant rodenticide, diphacinone sodium salt, a product with excellent efficacy for rodents but low toxicity for human beings and livestock. The product has been used throughout the country for many years and is highly appreci-

ated by the users for experimental and practical purposes. It has now become the leading rodenticide in the country. In 1996 the product was approved by the U.S. Environmental Protection Agency to enter the U.S. market and its efficacy has been proven in use.

Description of diphacinone sodium salt.

1. Yolk-coloured powder, odourless and tasteless.
2. Purity is 90%, soluble in ethyl alcohol, acetone and hot water, insoluble in benzene and toluene; solubility in water is 5%.
3. Noncorrosive, stable and suitable for long-term storage, no obvious melting point. When powder is exposed to 107–208°C, the colour changes from yellow to red. When exposed to 325°C, it decomposes.
4. It can be widely used to kill mice and rats in such places as houses, grain depots, chicken and cattle raising farms, stables, threshing grounds, food-processing factories, wharves and even ships and trains. It can also be used to poison rats in such areas as dry farmland, rice fields, forests, wasteland and grassland.

Characteristics of diphacinone sodium salt:

1. Strong effect. The chemical content of poison baits for mice or rats in the house or in the field is generally between 0.025–0.05%, with a maximum of 0.1%.
2. Low toxicity for human beings and livestock, but rabbits and cats are sensitive.
3. Excellent killing capacity, mortality rate is between 90–100%. It is a slow-acting poison.
4. Bait uptake by rats is high.
5. If accidental consumption of the poison occurs, an injection of the antidote, vitamin K₁, can be administered.

The rodent problem in farming areas and progress in its control in China

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About 30 species of rodents occur commonly in farming areas in China. The important species are *Apodemus agrarius*, *Cricetulus triton*, *Myospalax fontanieri*, *Rattus loseu*, *R. norvegicus* and *Mus musculus*. Population densities of these species have increased gradually since the beginning of the 1980s, and the damage caused in crops and grain storage has become an increasing problem, particularly for farmers. Since the 1990s, more than 25 Mha of crop have been damaged by rodents and this has affected about 150 million farmers. The grain losses caused by the rodents have been estimated at about 10 Mt/year. In 1983 the Chinese Government began to enhance the implementation of rodent pest control programs. The Ministry of Agriculture established the rodent-monitoring network, has strengthened research and has extended the integrated pest control methods for rodents. In

addition, a nationwide, united action for rodent control was carried out in the spring and autumn seasons. As a result, crop losses have significantly decreased with effective control of the rodents.

This paper discusses rodent occurrence and the progress of rodent pest management in the past 15 years and the potential for a more serious rodent pest infestation resulting from changes in cropping patterns, ecological factors and abnormal climatic conditions. A sustainable rodent management strategy is suggested as follows:

1. improve monitoring systems of rodent dynamics;
2. implement unified action for rodent control at a community level;
3. develop ecological and biological techniques for rodent control;
4. extend the use of anticoagulant rodenticides to replace acute rodenticides; and
5. promote training of extension staff at grass roots and farmer household level.

Integrated rodent control measures in demolition areas in the city of Shanghai

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This study investigated the implementation of integrated rodent control measures in demolition areas, comparing test and control zones. In test zones, the methods used were rodent killing, or a combination of rodent killing and prevention by improving the environmental sanitation. Three sites were chosen from different areas as test zones, and professionals were responsible for the environmental sanitation. At the first site, located at Changshou Road, rodent killing was attempted once only. At the second site, located at Jinjia Alley, a single rodent killing campaign was implemented and a rodent-prevention zone was established. At the third plot, located in the Huahui demolished area, the killing measures were applied twice, once before moving the residents and then after demolition of the buildings. A rodent prevention zone was also set up. In the control zone, located in the Shanghai Timber Mill demolished area, no control measures were taken. The variation between rodent densities was measured within and around the demolition sites. Damage caused by rodents in the surrounding areas was markedly reduced. Nevertheless, in the control zone, the rats increased by 5.07 times as measured by the powder track method, and increased by 3.98 times when the feeding method was applied. The results show that whether or not measures are taken to kill rodents in the demolished areas, there are striking differences in the intensities of rodent damage in the surrounding areas (powder track method: $t = 17.21$, $p < 0.01$; feeding method: $t = 16.48$, $p < 0.01$).

The dominant rodent, *Rattus flavipectus*, comprises 41% of the species in the demolition areas. If control measures were undertaken before demolition, and a rodent prevention zone was established, the surrounding areas experienced less damage than the control zone, or the areas where there was no rodent prevention

zone ($t = 3.94, p < 0.01$). If the rodent kill control measures were undertaken twice and there was also a rodent prevention zone, the damage in surrounding areas decreased by 66%. Therefore, a rodent killing campaign launched before the evacuation of the residents as well as after the demolition of old buildings, together with the establishment of a rodent prevention zone, may effectively control the spread of rodents from demolition districts.

Symposium E

Rodent chemical communication

PLENARY LECTURE

The olfactory world of the rodent

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Rodents live in an olfactory world and any attempt to understand rodent biology and management must understand the importance of olfaction for social behaviour, feeding, learning and orientation in the environment. This paper reviews research on the role of olfaction throughout the life of the rodent.

During prenatal development, the embryonic rodent is bathed in amniotic fluid, which imprints its odour on the infants. Olfaction is functional at the time of birth and infants are able to orientate to odours and make olfactory discriminations. Olfactory learning ability develops early in infancy and later the infants are attracted to the maternal odour, the odour of their littermates and to the odour of the food eaten by the parents.

The development of attraction to maternal and littermate odours is a form of 'olfactory imprinting' based on the genotype (MHC type) of the mother and siblings and on learned associations. After weaning, the young rodent learns to identify the sex and dominance status of other rodents by their odours and is able to learn food preferences and food aversions and to avoid predator odours. At puberty, rut odours develop and rodents learn by experience to discriminate sexually active from inactive conspecifics of the opposite sex. Odours are used for mate selection and the individual odours of mates are learned. Individual odours associated with dominant and subordinate conspecifics can also be learned. Following mating, females are able to discriminate between their own mate and an alien male, and mothers can discriminate between their own and alien infants by their odours.

Odours can modulate the reproductive system, facilitating or inhibiting puberty and reproductive behaviour, and modulating pregnancy. Predator odours activate defensive behaviours in rodents and rodents readily learn to associate odours with foods that make them sick, and they remember these odours for long periods. To orientate in their environment, rodents use scent marks. Thus, at each stage of their life, the social behaviour, food selection, and predator avoidance behaviour of the rodent depend on recognising and responding to olfactory stimuli.

ORAL PRESENTATIONS

Roles of gonadal hormones in the control of flank glands of rat-like hamsters (*Cricetulus triton*)

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Both male and female rat-like hamsters (*Cricetulus triton*) possess a pair of flank glands that are important for chemical communication. A preliminary study of the influence of the steroid hormones, androgen and/or oestrogen, on the size and secretion chemistry of flank glands of males or females was carried out.

Intact males and castrated males with implants of testosterone had significantly higher blood testosterone concentrations than that of castrated males ($p < 0.01$). Flank glands were significantly smaller after castration than those of either intact or castrated males with implants of testosterone ($p < 0.01$). The secretion of flank glands from castrated males was less attractive to females ($p < 0.01$). From gas chromatographic (GC) analysis, it was found that there were fewer chemical components in the secretions. These results demonstrate that testosterone can stimulate the size and secretion of male's flank gland and alter the attractiveness of the male to the female.

Intact females and ovariectomized females with oestradiol implants had significantly higher blood oestradiol concentrations than that of ovariectomized females ($p < 0.01$). The flank glands were significantly increased after ovariectomy and were significantly larger than those of both intact and ovariectomized females with oestradiol ($p < 0.01$). The secretion from flank glands of ovariectomized females was more attractive to males ($p < 0.01$) and GC analysis, showed the presence of more chemical components. These results demonstrate that oestradiol can decrease the size and secretion of the female's flank gland, and alter the attractiveness of the female to the male.

It seems that similar components in the secretions of flank glands were stimulated by testosterone in males and inhibited by oestradiol in females.

Influence of the vomeronasal organ on reproduction: chemosensory cues as potential regulators

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The vomeronasal organ (VNO) of rodents is a chemosensory structure in the nose. Its sensory neurones express genes for putative molecular receptors that are different

from those expressed within the olfactory epithelium. It is thought that these receptor proteins possess binding sites for chemical signals (ligands) that are species-specific pheromones and that these ligands elicit specific behavioural and/or physiological responses that have direct impact upon reproductive success of the organism.

Aims: In a series of experiments, we set out to determine whether: (1) the urine of male prairie voles (*Microtus ochrogaster*) stimulates activation of the reproductive axis of female prairie voles, which allows successful mating to occur; (2) activation of the reproductive axis of female prairie voles is affected by chemical signals from male mice (*Mus musculus*); (3) the female's vomeronasal system within the brain is activated by exposure to the urine from male prairie voles, but is not activated by urine from male mice; and (4) the VNO of the female prairie vole is essential for detecting the signals in the male's urine that activate the reproductive axis to the point of successful mating.

Methods: Unlike many other rodent species, the female vole does not have an oestrus cycle. Typically, the female's reproductive axis is quiescent and the uterus is unremarkable. It can, however, exhibit a hypertrophic response to activation of the reproductive axis. This can be measured by weighing the organ. Previous work demonstrated the importance of chemical signals for stimulating hypertrophy of the uterus. To determine whether a particular chemosensory stimulus activates neural pathways in the brain that are thought to carry relevant information, one can indirectly measure, by immunocytochemistry, activation of neurons by monitoring the expression of *fos*, a protein that is the product of early-immediate genes. Behavioural, e.g. mating, and/or physiological measures, i.e. hypertrophy of the uterus, to relevant chemical signals can be obtained from females who have an intact vomeronasal system or from females who lack the primary sensory afferents of this system after surgical removal of the VNO.

Results: (1) Urine from male voles activated the reproductive axis of females — uteri were hypertrophied, indicating that underlying hormonal pathways were stimulated. (2) The urine from male mice did not activate the reproductive axis of female voles—uteri were unremarkable. (3) The urine from male voles, but not from male mice, induced neural activity within the vomeronasal system of female voles—cells within specific brain regions that subserve the vomeronasal system stained positive for *fos* immunoreactivity. (4) Removal of the VNO from female voles impeded reproduction—most females failed to become pregnant, even during long-term cohabitation with males.

Discussion: The vomeronasal system appears to be a critical component of successful reproduction in female prairie voles and other rodents. If the molecular receptors within the VNO can be isolated, expressed and manipulated, or the ligands that would normally interact them altered to produce antagonists, they could serve as additional potential targets or devices in developing approaches for managing pest species.

Odours, scent over-marking and mate preferences

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Odours are particularly well suited as sources of information about potential mates, and we know that animals can obtain information from other individuals about conspecifics versus heterospecifics, sex, reproductive state, social status, individual identity, kin versus non-kin, etc. More recently we have shown, using two-choice odour preference tests, that several species of rodents detect and respond differentially toward potential mates on the basis of (1) day-to-day changes in reproductive state, (2) graded changes in hormone levels, (3) seasonal changes in odours associated with changes in hormonal condition, and (4) the quality of diet that has been consumed. From work in other laboratories we know that preferences may also be based on relative similarity of the major histocompatibility complex, the degree of parasitisation, and other factors.

In this talk I will review studies that suggest that scent marking behaviour may also provide information about the quality of a potential mate and that animals may use the extent and pattern of scent over-marks as a means of evaluating and preferring one individual over another. Scent over-marking occurs when one individual deposits its scent so that it at least partially covers the previous mark of another individual. The specific functions of scent over-marking have not been extensively investigated.

Both golden hamsters, *Mesocricetus auratus*, and meadow voles, *Microtus pennsylvanicus*, live solitarily during the breeding season. Home ranges overlap with several neighbours, and both males and females over-mark the scent marks of like-sex competitors. Such over-marking may be a means of competing with particular rivals—i.e. advertising oneself at the expense of the other individual. For an individual to continually keep its marks on top of one or more rivals should be energetically costly. Thus, over-marking would be an honest signal of vigour and phenotypic quality. Animals could use this only as a means to evaluate the relative quality of two individuals, but if they could determine the identity of two or more individuals from an over-mark, and furthermore if they could determine which individual had over-marked which other individual (that is, which individual had its marks on top). These abilities have not previously been demonstrated.

I report experiments showing that after exposure to scent over-marks, animals (both golden hamsters and meadow voles), show preferential memory for the top-scent of an over-mark. Investigations of how they do this suggest that they may use some as yet unknown cues from a region of overlap of two scents, and hamsters may also use the spatial arrangement of the two individuals marks. Surprisingly, they do not use, by itself, differences in scent age. We have also shown that, after exposure to scent over-marks of two opposite-sexed individuals, both male hamsters and male and female voles prefer to approach, investigate, and spend time near the individual that provided the top scent of the over-mark. Thus, hamsters and voles assess over-marks and prefer the top-scent individual; these preferences presumably reflect mate preferences.

These experiments emphasise the importance of scent over-marking for communication and competition between individuals. They also demonstrate previously unknown abilities of animals to analyse the topography of scent over-marks, and they suggest that these two rodent species use information contained in the pattern of over-marks to evaluate the quality of potential mates.

The role of conspecific and heterospecific chemical cues in population dynamics—an experimental approach

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Knowledge of the involvement of chemical cues on reproduction, a major factor influencing population dynamics, is restricted by conspecific odours. The aim of this study was to reveal a possible impact of odour cues on reproduction of model rodent species. Particular attention has been paid to heterospecific chemical cues such as odours of closely related species and unrelated species including predators. As the model species, hamsters of *Phodopus* genus and golden hamster (*Mesocricetus auratus*) that vary in their level of sociality, and Mongolian gerbils (*Meriones unguiculatus*) were used. The data obtained showed that in spite of differences in social organisation conspecific odour cues strongly influence the rate of reproductive development of juveniles. The chemical cues from closely related species were found to direct the rate of sexual maturation of juveniles to the same extent as conspecific ones. Odours of species of different genes were found ineffective in influencing the maturation rate. In general, predator odours had a negative influence on breeding of all species studied, leading to suppression of the efficiency of reproduction and the rate of maturation of juveniles. However, from a long-term perspective such an influence may have a positive profound impact on survival rate and future reproduction of potential prey. These data show that chemical cues are important factors of population dynamics in Cricetinae and Gerbellinae.

Social environment in relation with the reproductive success of females in two vole species

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In western Europe, bank voles (*Clethrionomys glareolus*) undergo seasonal population fluctuations at relatively low local densities. Common voles (*Microtus arvalis*), on the contrary, undergo very high annual and pluri-annual population fluctuations and, in some years, they become a major agricultural pest. Ecological data indicate that during the breeding season, the social organisations of these two species markedly differ. In bank voles, breeding females are solitary and hold exclusive territories while males form stable hierarchical groups. The home ranges of dominant males are larger than those of subordinates and overlap those of several females.

In common voles, most breeding females live in exclusive groups of 2 to 6 and share large common burrows. The social position of males in relation to these groups is unknown. We hypothesised that differences in the reproductive success between females of these two species rely, at least partly, on their spacing behaviour and on the parental investment. The experiments reported here were aimed at testing this hypothesis under laboratory conditions. Unfamiliar and unrelated, non-breeding females as well as familiar and related females (mothers-and-daughters or sisters) were kept in pairs for several weeks in large complex enclosures provided with individual artificial burrows. Their social behaviour was analysed throughout a reproductive cycle, from sexual quiescence to lactation.

Unrelated female bank voles exhibited friendly behaviour until the middle of pregnancy, sharing the same nest. In late pregnancy, females became aggressive and solitary.

In common voles, spacing behaviour between unrelated females occurred in early pregnancy and was far more aggressive than in the former species. However, in most pairs of both species, the reproduction of one female was suppressed.

In pairs of related female bank voles, pregnancy failure was far more frequent than among unrelated individuals. In contrast, in pairs of common voles, all related females did reproduce. These results strongly suggest that, in the field, grouped breeding female common voles are genetically related.

The fine analysis of behaviour revealed that the exclusion from procreation did not result from mate selection by the male and suggested that, without any possibility of dispersion, stress and pheromones picked up during female–female contacts may interfere with the physiology of breeding. These effects could be one of the density-dependent factors that may temporarily decrease reproductive success of females in the open, at high population densities. They may take place in groups of related female common voles but only in very crowded groups sharing the same burrows.

Our very recent experiments suggest that differences in parental behaviour are another factor which may explain the high fertility of common voles.

The role of predator cues in reproduction of Norway rats

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The behaviour of prey can be changed dramatically by the presence of predator. Chem-
osensory detection may be an important aspect of the predator-avoidance strategy of
many mammals. Small mammals tend to avoid predator odours. Recent studies have
stressed the potential of predator scents as natural repellents. Such odours have been
used in the laboratory and in the field to repel herbivores and to reduce feeding damage
to a variety of plants. Despite the increasing number of publications concerning the

problem of predator-prey chemical communication over recent decades, virtually nothing is known about how predator odour influences the reproductive status and reproductive success of prey. In our experiments we tested the efficiency of the action of chemical cues from sympatric and allopatric predators on reproductive status and final reproductive success of Norway rats. Urine from cats (*Felis catus*) kept on a strict meat diet, urine from coyotes (*Canis latrans*) and anal mink secretions (*Mustela vison*) were used as a source of predator chemical cues. The influence of predator chemical cues on a rat sexual behaviour and on the final reproductive success was evaluated in a number of tests. Mink secretions apparently caused an extension of the oestrus cycle for 4–12 days (1–3 complete cycles) when they were applied to the bedding of rats in metoestrus. However, the apparent expression of the effect may depend in part on the age of the secretions. Mink secretions also tended to be the most effective (among tested chemical cues) for suppression of male's sexual behaviour. Although rats responded to scents from allopatric predators, chemical cues from sympatric species tended to be more effective. Responses to chemical cues derived from non-native predators do not involve recognition of the predator as a species. They may be due to a common carnivore signal, sulfur-containing odorants, produced during the digestion of meat and fat. Removal of sulfur-containing compounds from the cat and coyote urine completely suppressed the behavioural response of Norway rats to these chemical signals. The total number of offspring of rats exposed to predator odours was considerably lower relative to control animals. Average litter size in the control group was double that of the experimental group. Exposures to predator odours also led to disturbances in sex ratio. The response of predator-naive laboratory rats to predator chemical cues and the failure to habituate to these signals can be interpreted as evidence that responses to these stimuli are innate. Exposure to predator odours for 48 hours after mating was sufficient to produce effects on litter size and sex ratio, while the same length exposures during midgestational period did not produce negative effect. We propose the hypothesis that predator urine affects hormonal mechanisms that regulate implantation of rodent embryos shortly after fertilisation. If predator odours act as reproductive disruptors, these findings will pave the way to control rodent populations and their economic impact on agricultural production, without having to resort to toxicants and other artificial chemical systems.

Hierarchical structures, regulation of reproduction, odour preferences and susceptibility to diseases in groups of female common voles, *Microtus arvalis*

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At present, research on population dynamics of rodents lacks sufficient studies on female-female interactions. In species where females live in unisexual breeding groups, dominance-subordinate relationships may be one factor in regulating reproduction and distribution of rodent populations. For the common vole, *Microtus arvalis*, our studies show that the relatedness between females of a breeding group determines the form of established hierarchies in these groups and affects their repro-

ductive success. By using non-metabolisable dyes to recognise urine marks, results showed that the intensity of urine marking and reproductive activity of individual females in female groups were positively correlated. This indicates that dominance in female groups of *M. arvalis* is associated with both advertising home range and reproductive success. The variability in the intensity of reproduction in cyclic populations of *M. arvalis* may therefore be attributable to changes in the degree of relatedness between females in breeding groups of *M. arvalis* with increasing population density.

In mother–daughter groups, young females are reproductively suppressed by their mothers which is manifested more by a failed implantation or abortion, than by the delay or inhibition of oestrus in young females. The dispersal behaviour of young, reproductively suppressed females from their mothers was tested in groups of two adult females and four of their daughters in large enclosures. Young females tend to be more frequently outside the initial home area of the enclosure than their mothers. Giving them the choice between an area scented by odour cues from related or unrelated females, they most frequently choose the side with the related odour. Female common voles avoid areas with odours from predators. However, young female *M. arvalis*, which do not leave their mother's nest, help protect the new pups of their mothers. Their help is restricted to the transport of the pups back to the nest, but does not include the formation or improvement of nests. In helping their mothers, young females may benefit more than from dispersal. This behaviour guarantees the rapid population growth seen in *M. arvalis*.

At high population density, young females may have to leave their natal site in search of their own nesting places. These dispersing young females are potential vectors for the transmission of rodent-borne diseases to humans. Experiments that tested differences in the specific immune response of females to sheep red blood cells in breeding groups of *M. arvalis*, reveal that young females show a higher immune response than their mothers. As this could also be shown in non-reproducing groups of females, our findings indicate the existence of a hierarchy-related immunosuppression in female *M. arvalis*. The presented results are fundamental to the understanding of dispersal in rodent populations and will assist in the development of biological methods to control reproduction and dispersal of rodents in order to limit the transmission of rodent-borne diseases to humans.

Olfactory communication in Brandt's vole: individual odour discrimination in mate choice

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Olfactory cues underlie social discrimination in microtine rodents and appear to mediate many aspects of social behaviour. The adult Brandt's vole, *Microtus brandti*, was specifically studied to investigate its ability to discriminate individuals and to determine the mating system of this species. In a 30-minute test, female voles demonstrated more social investigations of foreign male odours than of odours of their partner. However, they also spent more time in self-grooming, resting, and staying in

the box with their own partner's odour in the substrate, while avoiding unfamiliar male odours. Virgin adult females showed more sniffing and licking behaviour towards wood-shavings containing the odours of subordinates than of those belonging to the dominant male. They showed no significant differences in other behaviours. Male voles preferred the odours of oestrous females to those of non-oestrous females. During an oestrous cycle, a novel female's odour was more attractive to the male than his own partner's odour.

The results indicate that adult Brandt's voles have the ability to discriminate between different individuals of the opposite sex by using chemical scents. It is also suggested that the principal mating system of Brandt's voles might be polygyny.

Olfactory and cognitive abilities in senile Wistar rats

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For more than 70 years scientists have debated whether learning ability is reduced in old animals. Most of the research was done with rats, with variable results. When discussing these differences it was argued that the different results might be due to different experimental setups and/or that differences in learning or cognitive abilities can only be shown when the task is complex enough. Without any doubt, the physical abilities diminish with age in adult animals and the senses become less sensitive. In our studies with rats we therefore chose an experimental set-up, which does not require much locomotory activity of the animal. This was done to ensure that physical condition will not influence the performance of the learning task.

An olfactory Skinner-box seemed to fit our demands. The animal is allowed to sit or to lie in the testing chamber while performing the task. The demand on the animal was to respond to a specific odour (S+) presented via a testing tube attached to one side of the chamber while air or a second odour (S-) should be ignored. After odour presentation (S+) and correct identification the animal had access to a water reward. Mistakes were neither rewarded nor punished.

For our study 2, 27 and 32-month old male Wistar rats were used. First, we looked for possible age dependent differences (time needed, number of mistakes) before learning criterion (90% correct responses) was reached. No significant differences between the ages were found. According to earlier studies by other researchers rats are able to create a learning-set when they have to discriminate between pairs of odours. In the following experiments we therefore concentrated on whether senile rats are able to build up a learning-set too. In this advanced form of learning we presented to 28-month old animals and 3-month old controls five different pairs of odourants at fairly high concentrations (0.2% vol), one of the odours being rewarded (S+) the other one not (S-). Each pair was presented for one session only (100 trials), and only one session per day was performed. For the first pair the same odour was used as S+ as in the initial training when the animals had to learn the discrimination task; S-

was unknown. For sessions 2 to 5 either the odour used as S+ or S- was new to the rats. During the five sessions the rats improved their performance as indicated by the decreasing number of mistakes: in session 1 there were 7.69 mistakes on the average, in session 5 only 1.77 mistakes ($p < 0.05$). Thus, a learning set was established already during these few experiments. Again no difference in performance between young and senile rats could be detected. We conclude that there is no diminished learning or cognitive ability in senile rats.

POSTER PRESENTATIONS

Influence of cat urinary chemosignals on maturation, testosterone level and meiosis in male Campbell's hamsters (*Phodopus campbelli*)

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Only few studies have tried to estimate the influence of predator odours on reproduction and population dynamics of their potential prey. The present study was conducted: 1) to reveal a possible role of cat urine (CU) in regulating the development in Campbell hamster males (*Phodopus campbelli*); 2) to analyse the testosterone level in CU-treated males; and 3) to check whether CU influences meiosis in prepubertal males. Males were treated every other day from postnatal day 11 until 30 by having cat urine (experimental group) or water (control group) applied directly onto the external nares and around the lips. After termination of the experiment, at the age of one month, the weights of the body, testes, epididymis and adrenal gland were obtained. The results revealed:

1. experimental males had significantly lower body weights than control males ($p < 0.01$). However, there were no significant differences in testes weights and testes weights corrected for body weights. In CU-exposed males epididymis weights ($p < 0.01$) as well as epididymis weights corrected for body weights ($p < 0.05$) were significantly lower than in control animals. There was no obvious difference between experimental and control groups in adrenal gland weights; yet, adrenal gland weights corrected for body weights were significantly higher in CU-treated males ($p < 0.05$).
2. In the experimental group, testosterone concentration in the urine was 0.010 ng/mL while in the control group the testosterone concentration amounted to 0.233 ng/mL.
3. Electron microscopic analysis of the pachytene nuclei in the control group revealed no abnormalities of the synaptonemal complexes in both sex chromosomes and autosomes. However, in the experimental group in 12.5% of the cells an abnormal configuration of SC was found ($p < 0.001$). The anomalies included

autosomal terminal asynapsis, interstitial autosomal asynapsis combined with interlocking, and sex chromosome dissociation. These data indicate that CU influences the development of some organ weights and the testosterone level in prepubertal males and corresponds with the development and meiosis disturbance.

Plasticity of rodent chemical communication

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Chemical communication influences population dynamics, species diversity, ecosystem balance, individual reproductive success, inter- and intraspecific competition, territoriality, and access to habitat and nutrients. The olfactory epithelium and the vomeronasal organ extract information from chemical signals. Via these sensory pathways, chemical signals may alter the onset of puberty, block pregnancies, synchronise breeding cycles, alter hormone levels, and provide information about territory, the dominance and health status of the signalling animal, reproductive state, and individual identity. Unlike many other sensory systems, nasal chemoreception appears to be dynamic across the lifetime of an organism. Individual experiences with odours interact with genetic propensities to yield a measurable phenotype. Using rodents as model systems, we have determined that inbred strains of mice provide an excellent genetic model of variation in sensitivity to the mammalian pheromones. These mice could be sensitised to the mammalian pheromone androstenone (AND), regardless of their initial level of sensitivity or insensitivity to the compound. Such induction is correlated with changes in the sensory epithelium as determined biochemically and electrophysiologically. Using different, unrelated odorants and complex mixtures, such as conspecific and heterospecific urine, we have shown that induced olfactory sensitivity is a general phenomenon, which reflects the plasticity of animal chemical communication. Modulation of olfactory sensitivity by environmental factors, as well as induction of sensitivity to odorants and con- and heterospecific excretions, considerably influences an organism's adaptability. In separate studies, manipulation of the odour environment in *Mus musculus* and *Rattus norvegicus* revealed a critical period in neonatal development for imprinting odour. Relative to age-matched controls AND exposures during days (14–28) after birth produced >600 fold increase in sensitivity to AND, while the same exposures during adulthood or during days 1–16, 28–42 after birth produced a 16-fold increase in sensitivity. These results are consistent with previous findings with rats and mice, which revealed a similar critical period during days 14–28 for affecting sensitivity to and recognition of individual-specific urine in adulthood. Induced sensitivity to odorants and complex mixtures such as conspecific or heterospecific urine persisted for relatively long periods. In our experiments with AND elevated sensitivity to the compound was recorded 8.5 months after exposure. Exposure to odorants of older animals (1 year or older) did not considerably affect sensitivity to these odours. Hence, it appears that there is a critical period 2 weeks after birth, just after the eyes open, during which

odour imprinting can be modulated. Developmental changes in olfactory sensitivity and possible mechanisms of induced olfactory sensitivity during different life periods are discussed.

Sexual differences and seasonal changes in size of flank glands of rat-like hamsters (*Cricetulus triton*)

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The length, width and thickness of flank glands of wild adult rat-like hamsters (*Cricetulus triton*) were positively correlated with body weight or testes weight during the breeding season ($p < 0.001$), and with body weight ($p < 0.001$) but not with testes weight ($p > 0.05$) during the non-breeding season. The dimensions of the gland were significantly different between the sexes during the breeding season ($p < 0.01$) and significantly different between seasons in the males ($p < 0.05$). For females there were no significant differences in the gland size during the non-breeding and breeding seasons ($p > 0.05$).

These results show that body weight and testes weight can affect flank gland size independently. Also the seasonal changes and sexual differences in the flank gland were related to the seasonal changes in reproductive state and function of flank gland.

Symposium F

Rodent Behaviour and Implication in Management

PLENARY LECTURE

The brown rat: explorations of opportunism

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The brown rat, *Rattus norvegicus*, is an exceptionally successful opportunist, and its success is not merely fascinating for students of adaptation, but also poses a challenge to agriculture and public health. Yet, there have been surprisingly few studies of the behaviour of wild rats and much remains unknown about the intricacy of rat behaviour and ecology. Our team at Oxford has been involved in studies of rat behaviour for a decade, and in this paper we synthesise our findings on the behaviour of farm rats, their diseases, neophobia, anti-predator behaviour and social system. We interpret these findings in terms of both the evolution of rats and their management.

Our presentation falls into a series of related sections.

First, we consider what is known of the behavioural ecology of wild rats in the field. We have studied the demography of farm rat populations around Oxford and have radio-tracked rats in the wild. Population structure, home range size and activity patterns all differ between populations. In particular, we describe one population where nocturnal risk of predation from foxes appears to be responsible for the rats switching to diurnal activity.

Second we explore aspects of food selection and neophobia. In particular we describe an automated apparatus that enabled us to log the feeding bouts of rats in a large enclosure. It emerged that rats differ in their tendency to show pre- or postprandial feeding correlations, in terms of season, sex and social status. These results accord with studies in experimental psychology.

Third, we review our work on neophobia in the field, where some individuals may avoid novel baits for as much as 40 days. We note that neophobia is reduced in individuals infected with the parasite *Toxoplasma gondii*. This leads us, fourthly, to a review of pathogens of farmland rats. We record, for the first time in the U.K., both Hantaan virus and Q fever in wild rats. Rats infected with *Toxoplasma* lose their fear of cat odours and indeed may seek out this predatory odour. This is likely to be a case of parasite-altered behaviour that ensures that the parasite completes its life cycle between rat and cat.

Finally, we report a new form of warfarin resistance that appears to offer heterozygote advantage even in the absence of poison.

ORAL PRESENTATIONS

Bark consumption by South African rodents and its implications for commercial pine forestry

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Studies in Scandinavia in particular have found that bark consumption by small rodents peaks in winter and seems linked to high population densities of voles and the mineral content of the bark. In most of these cases the bark consumption occurs under deep snow. In contrast, bark consumption in South Africa is not linked to season but appears linked to rainfall and occurs during the dry season in both summer and winter rainfall regions. The aim of this study is to examine the factors which might induce bark-eating behaviour in rodents.

A study was made of the food value, moisture and mineral content of the bark of a variety of indigenous trees, shrubs occurring in eastern thorn bushveld, and compared with nutritional data obtained for grasses. Results indicate that bark consumption starts as soon as rainfall ends and the moisture content of the grasses drops. The bark moisture content of the preferred trees and shrubs remains relatively high (> 40%) throughout the dry season. The results for mineral content and food value are equivocal. Preliminary results appear to indicate that the intensity of bark consumption is linked to population density but that consumption does occur at low densities.

The significance of bark consumption in a natural system appears to be ecological and when taken in conjunction with fire it appears to play a role in reducing bush encroachment of grassland. Three widely distributed rodent species have been implicated in bark consumption in South Africa: *Rhabdomys pumilio*, *Otomys irroratus* and *Mastomys natalensis*.

In commercial pine forestry, bark consumption takes on an economic significance. Damage to young pine saplings (< 4 years old) costs the industry over R50 million per annum and this increases in years of drought, which are linked to the El Niño Southern Oscillation phenomenon. The response of the forestry industry to this damage is widespread poisoning using 'super-wafarins' and with this goes the risk of secondary poisoning of carnivores and raptors. Furthermore, poisoning is a temporary solution and has to be repeated until the wet season starts. Commercial forestry is very important in South Africa as the country has very little indigenous forest.

A fuller understanding of the reasons underlying bark consumption should assist in formulating an appropriate control strategy for these rodents in commercial forests.

Arboreal behaviour of the Japanese dormouse (*Glirulus japonicus*)

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Arboreal behaviour is a feature characterising Gliridae. Therefore, in studying their life histories, it is important to understand their arboreal behaviour. The Japanese dormouse, *Glirulus japonicus*, is a species endemic to Japan and is designated as a natural monument. In the present study, the arboreal behaviour of the Japanese dormouse was observed by using luminous material attached to the dorsum of the animal. The study was conducted from 1992 through to 1998 in a deciduous forest at an altitude of 1500 m. The arboreal behaviour of 20 animals was observed. The Japanese dormouse showed the following characteristics in its arboreal behaviour:

1. it moved very quickly;
2. it often walked on the undersides of branches;
3. it often jumped about 30 cm from trunk to trunk; and
4. it moved along the same arboreal course twice or three times during a night.

The arboreal behaviour of the Japanese dormouse showed a pattern characterised by staying in certain trees for feeding and moving very quickly between these trees. Individual animals were observed to feed on the bark of dead branches of *Malus sieboldii*; flowers of *Larix leptolepis*, *Clethra barbinervis* and *Enkianthus campanulatus*; seeds of *Picea jezoensis*; and insects. The Japanese dormouse fed on the bark of *M. sieboldii* through the active season, indicating that this bark is an important food for the animal. It seems that food for dormice is not in abundance in the forest throughout the year, and hence the population cannot increase to high numbers.

A method for studying behaviour of small animals

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Many kinds of equipment including simple mazes, large arenas, mechanical treadles and computer recording systems have been used to study the behaviour of small animals in the laboratory.

We have designed an advanced and complex area for researching behaviours of small animals. It includes an arena with 4 basements (each 6 m × 4 m). Depending on the species and the aims of experiments, each arena can include nests, tunnels and active areas. Environmental factors, such as light regimes, temperature variation, and noise level, can also be controlled. The observation room holds the equipment for recording the behaviour of small animals including infrared light closed-circuit videotape, remote television, infrared light sensors and computers. The distance from the basements and

observation room is 30 m and information about the animals' behaviour is transferred electronically. Noise and other possible disturbing factors which may influence the animals are avoided so that the observed behaviour is as natural as possible.

From 1987 to 1998, we successfully studied the behaviour of rats, plateau pika (*Ochotona curzoniae*), plateau zokor (*Myospalax baileyi*), polecat (*Mustela evermanni*) and weasel (*M. altaica*). The basement areas were excellent for studying the effects of different odours, light regimes, food habits and predator influences.

We suggest that some more general features could be incorporated into the design for researching the behaviour of wild small animals.

1. Study arenas must be large enough to allow animals to behave naturally.
2. Little or no training should be required to record responses of test animals. Responses observed should be validated and simulated if possible. What would occur in a natural situation?
3. Disturbance should be reduced to allow animals to behave naturally.
4. If more than one factor (odour) is to be tested, carryover effects should be eliminated so that the results can be interpreted concisely. For odour tests, exhaust fans may be required.
5. The methods for observing the animal's behaviour must be specific enough to assure accurate interpretations of the behaviour. The animal should not be aware of the sensing method.
6. The study arenas and testing procedures should be designed so that replications and statistical analysis can be performed accurately.

A comparative analysis of behaviour between two sympatric species, *Ochotona daurica* and *Ochotona curzoniae*

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The sympatric coexistence of *Ochotona curzoniae* and *O. daurica* was found at Nian-nosoma area of Gangcha County, Qinghai Province (37°10'N, 49°40'E). To heighten our understanding of the diversity, adaptation and mechanisms of pika's behaviour, we observed the behaviours of the two pika species in a comparative study. We marked 40 *O. daurica* and 30 *O. curzoniae* in a 0.5 km² study area. Focal animal sampling at 30 second intervals during 15 minute observations of each animal was used to describe 9 non-social behaviours and 14 social behaviours. For non-social behaviour, the pattern of alert behaviour of the two pika species was different. *O. daurica* shows hoarding behaviour, while *O. curzoniae* shows mowing behaviour. These behaviours are different to those where the species are not sympatric.

For *O. daurica*, non-social behaviour comprises 96% of all observed behaviours. For *O. curzoniae*, non-social behaviour comprised 87%. The frequency of non-social behaviour was significantly different between the two pika species ($X^2 = 7.06$, $X^2 > X^2_{0.01}$). Feeding is the most common non-social behaviour in two pika species. There was a significant difference in the frequency of social behaviours between the two species ($X^2 = 87.7$, $X^2 > X^2_{0.01}$). *O. curzoniae* spent more time in social interactions.

Of the social behaviours, affiliative behaviour by *O. curzoniae* was the most common comprising 75% of all observed social interactions. The second most common was play-like behaviour, and the least common was aggressive behaviour and comprised 10%. By contrast, aggressive behaviour of *O. daurica* was the most common social behaviour and comprised 61% of the all observed social behaviours, the second was affiliative behaviour, with play-behaviour least at just over 5%. *O. curzoniae* is more social than *O. daurica*, while the aggressive character of individuals in *O. daurica* population was stronger than that in *O. curzoniae* populations.

Studies of the social behaviour in colonies of Brandt's vole (*Microtus Brandti*)

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Social interactions in colonies of Brandt's vole were studied in the field and laboratory from August 1995 to October 1996. The results show that it is important to have ongoing behavioural interactions to maintain steady social structures in the colonies. There are two periods of social interaction in the colony. One is during the period of reproduction, when more than 50% of the voles (most are sub-adults and male adults) move into strange colonies. Another is in the non-reproduction period, when only a few voles move into strange colonies. Most colonies have social hierarchies. Juveniles born in July or August remain in their colony until next spring and assist adults with storing grass.

There are three possible responses when a vole meets another unknown vole: acceptance of each other, tolerance or refusal. An unknown vole may be accepted during the reproduction period, or be tolerated, with disputes possible between two males. During the non-breeding period a stranger is refused or is tolerated. Disputes occur if the same sex feed together.

It was also discovered that the juveniles (7–10 g) grow at different rates if they have been with a different partner. The vole with its mother grows quickly during the first 20 days. After then the voles will grow better in strange colony.

Studies of aggressive behaviour of plateau pika in the reproductive period

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It is generally acknowledged that aggressive interactions result in dispersion, inhibition of reproductive functions or death. These interactions play a major role in shaping social structure, mating systems and spatial distribution of rodents. The plateau pika (*Ochotona curzoniae*) is a social animal, and different opinions exist about its mating system. This paper mainly deals with the aggressive behaviour of plateau pika in the reproductive period by studying female–female, female–male, and male–male interactions in the laboratory in order to determine its mating system. A total of 20 individuals was used in the experiment: 10 females and 10 males. The animal's behaviour was automatically recorded by videotape. The following findings were made.

1. Both females and males had the same aggressive abilities with inter-sex aggression being higher than that of intra-sex.
2. Interactions with unfamiliar individuals caused females first to display 'attack and chase' aggressive behaviour and second to change to alternate defensive and amicable behaviour if it was a male, or to use defensive behaviour if it was another female.
3. The pattern of male behaviour is that males first display attack, chase and offensive positions when approached by an unfamiliar individual. They then change to an amicable behaviour if approached by a female, or display a high attack, chase and offensive position if approached by another male.
4. This indicated that the pika can regulate its behaviour according to its interactions with different individuals. The females and males may actively select their mates. The mating system may allow monogamy, polygamy and polyandry together in natural populations because of this aggressive behaviour. The high degree of polygamy may arise from high aggression in males.

Familiarity and mate choice of female and male root voles, *Microtus oeconomus*

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Comparative behavioural experiments between monogamous and polygamous species of microtine rodents show that the mating systems are associated with inter-sexual mate choice among individuals. A major component determining the nature of this sexual selection is familiarity between males and females.

Long and short-term effects of familiarity of both sexes on mate choices in the root vole (*Microtus oeconomus*) were examined. Experiments included female mate choices for the familiar versus the unfamiliar, their partner versus unfamiliar males and their partner versus familiar males. Similarly, male mate choice was determined with familiar versus unfamiliar partners and their partner versus unfamiliar females. Familiarity was established by housing a female with a male in the same cage for 8 days before a trial. A partnership was defined by the production of at least one litter by a pair of voles.

To conduct a trial, two voles were tethered between two chambers of a T-shaped maze. Another vole was placed in the central arena of the maze and interactions were scored. An observer recorded the duration and frequency of visits, social-investigations, copulation, aggression and amicable behaviours between each of the voles. Statistical analyses were performed using the Wilcoxon matched-pairs test. The results showed that females preferred familiar to unfamiliar males, their partner to unfamiliar males and their partner to familiar males. However, the males had no preference either for familiar versus unfamiliar females or for their partner versus unfamiliar females. These results suggest that the female root vole's preference for familiar males and the males lack of preference in mate choice may be a proximate behavioural process underlying this species' mating system. Thus, female monogamy and male polygamy could be explained only by the hypothesis that the mating system is polygynous in root voles.

POSTER PRESENTATIONS

Incest-avoiding behaviour of Levant's vole (*Microtus guentheri*) in captivity

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Since inbreeding harms the population, many plants and animals have adapted to avoid this phenomenon. In rodents this is usually expressed by suppressing the reproduction of offspring in family groups (mole rats, prairie dogs), or by ensuring adult males and females leave before they are mature (white-footed mouse and others). The effect of these activities was not found to be absolute and varied in the species. Levant voles were observed to display incest-avoiding behaviour in about 70% of cases. In most of the groups of voles that were weaned at the same time (imitating a non-divided litter), the animals did not reproduce, although they matured at the usual time. The pairs that consisted of voles reared after being weaned together (in the same cage) were usually sterile, whereas the same animals paired with those of other groups successfully reproduced from the age of 6-7 weeks. However, after being separated for about 3 weeks, the voles that were reared together mated with their daughters if they remained in family groups. In contrast, the house mice, both wild and laboratory, do not show any incest-avoiding behaviour in some animals and its absence in others has not yet been clarified.

A battery operated animal activity recording system with a single-chip microcomputer programmed in BASIC language

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Many animals are nocturnal and secretive. It is useful to have an animal activity recorder to study the activity and related behaviour of animals in the field. However, making these recorders is very expensive. The existing systems cannot be used readily in the field, are too expensive or working duration of the battery is too short.

This paper reports an animal activity recording system, which has been used in our rodent activity research. The system is operated by a single-chip microcomputer, which can run for days with a battery in the field; the running duration with a battery depends mainly on the kinds sensors connected. Single-chip microcomputers are designed for industrial purposes, so they can work reliably in harsh environments, and one model will be produced at least for many years. The model used in our system is a streamlined model with RISC construction, the program language is BASIC instead of machine code or assembly language. BASIC is one of the most popular program languages among scientists. The application program is written and edited in an IBM-PC compatible and debugged online then transferred to and stored in the single-chip microcomputer, the single-chip microcomputer will run independently. The user can easily modify the program to special work mode. The I2C bus is used in the system. The RISC single-chip microcomputer and the I2C bus make the system more simple and reliable with small size, light weight and low power consumption.

The system is compatible with many sensors such as infrared sensors, mechanical switches and magnetic sensors. From 1 to 14 sensors can be connected to the system. The occurrence and frequency of animal activity can be recorded. The data acquired can be stored in the IC card, or printed out directly. The data stored in the IC card can be outputted later in three ways with the IC card reader of the system, which is also operated with the same mode single-chip microcomputer. One is transferred to an IBM compatible PC or read out from the LCD panel of the reader.

The data acquired with the system in the rodent activity research conducted in Chengdu are presented in the paper.

The social structure and mating system of Brandt's vole (*Microtus brandti*)

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This study was conducted in the typical steppe of the Inner Mongolian grassland from 1995 to 1998. We used capture-mark-recapture and direct sighting techniques to census the wild populations of Brandt's vole (*Microtus brandti*) in two plots: a

natural sample plot (43°25', 116°41'), and an enclosure plot (43°37', 116°41'). Many studies of the social structure and mating system have been completed.

Our data have revealed that Brandt's voles live in family units or groups throughout the year. In the winter, the communal group usually consists of 5–20 voles of mixed sex and age. These family units regroup in the early spring when reproduction starts. During this period, all of the males that over-wintered disperse from the original winter nest and the average dispersal distance is greater than 120 m. Most of the over-wintered females remain in the nest or move to neighbouring territories and the average dispersal distance is about 20–30 m. In the following breeding season, the family group is relatively stable. A family usually consists of the founding over-wintered male, over-wintered female(s) and their offspring. Most of the offspring will stay in their territory except for a few males which, when they reach sexual maturation, will disperse. The over-wintered males are dominant and drive off any other males with scrotal testes in their territories. At the end of the breeding season, family groups with too many members usually break off into several groups. These reformed groups may also comprise some voles that come from an adjacent group. But the average reformation rate of these groups is very low (about 0.1) during that period. Most members of a communal winter group come from the same original families.

There is evidence that the mating system of the Brandt's vole is polygynous. Translocation experiments that have been done in the enclosure area have revealed that while only one mature male can live in a family unit, many mature females can live and reproduce in the same group during the breeding season. This result is strongly supported by the capture–recapture records from the wild populations. Furthermore the sex ratio of mature voles indicates that a male copulates with more than one female in the breeding season. The social hierarchy and the territorial behaviour of the over-winter males also suggests a typical polygynous mating system.

The effect of kinship on social behaviour of Brandt's voles *(Microtus brandti)*

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It has become more and more obvious that kinship influences the lives of animals since the 'Kin Selection' hypothesis was proposed in 1960s. The role of kinship in Brandt's voles (*Microtus brandti*) in agonistic behaviour, mate choice and parental care was evaluated using testing chambers and breeding cages. We examined agonistic behaviour and social investigation between unfamiliar siblings and nonsiblings. No significant kin bias by the experimental animals was found. Males sniffed and followed the unfamiliar, unrelated females significantly more than they did with their unfamiliar sibling sisters, but they did not show a significant preference in copulatory behaviour and agonistic behaviour. While females did not display significant kin bias in social investigation, they spent significantly more time copulating with the unfamiliar, unrelated males than with their unfamiliar sibling brothers.

Pup development was divided into five periods: period 1 (newborn: 1–5 days), period 2 (ears erecting: 6–9 days), period 3 (eyes opening: 10–14 days), period 4 (eating solid food: 15–20 days), period 5 (weaning: 21–24 days). Males did not show any significant kin bias in paternal behaviour, while females sniffed the unfamiliar unrelated pups significantly more than the unfamiliar nieces/nephews during periods 2 and 3. The parents displayed infanticide of their unfamiliar nieces/nephews or unfamiliar, unrelated pups once the pups were able to eat the solid food. However, no evidence from the present study indicated that males and females could regulate the infanticide based on kinship.

These results suggest that kinship influences the social behaviour of Brandt's voles, especially inbreeding avoidance, in maternal care during the specific periods (6–14 days) of the pup development.

Seasonal differences in social behaviour among adult rat-like hamsters (*Cricetulus triton*)

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The objectives of this study were to describe the behavioural interactions of adult rat-like hamsters (*Cricetulus triton*) in intra- and intersexual encounters in a neutral arena, and social preference in a Y maze during the non-breeding season and the breeding season, and to determine whether the hamster is solitary.

During both the non-breeding and the breeding seasons, both males and females preferred to associate with individual con-specifics than a control (empty) Y maze. This implied that there usually were social interactions among solitary individuals. In the Y maze, tests between male and female individuals, showed that focal males preferred males to females during the non-breeding season and did not show a sexual preference during the breeding season; focal females did not display sexual preferences during either season. These results indicate that although there were frequent social interactions, permanent and close pairs were not formed. The non-breeding males' preference for male con-specifics may be motivated by aggression. The above results support the view that rat-like hamsters are solitary.

For staged paired encounters in a neutral arena, the social interactions mainly consisted of agonistic acts and investigation. Encounters between same sexes included frequent agonistic acts and no amicable acts, where the victors showed more attacks, were less defensive and showed more flank gland marking ($p < 0.05$ or $p < 0.01$) during each season. In female–male encounters, females always defeated male opponents during the non-breeding season, showing more aggression, less defensive behaviour and more flank marking than males ($p < 0.05$). There were no significant differences in these behaviours between breeding males and dioestrous female encounters ($p > 0.05$).

The results imply that the hamster is solitary and does not form permanent and close pairs. Flank gland marking was positively related to agonistic behaviour and dominant status during each season. Breeding encounters were more frequent than non-breeding encounters ($p < 0.05$ or $p < 0.01$). Non-breeding male–female or female–female encounters showed more mutual aggression than breeding season encounters ($p < 0.05$ or $p < 0.01$). There were no between-season differences in mutual aggression between male–male encounters ($p > 0.05$). The results may be due to seasonal changes in reproductive status.

Symposium G

Epidemiology of Rodent Diseases and Their Impact on Rodent Population and Humans

PLENARY LECTURE

The role of rodents in emerging human disease: examples from the hantaviruses and arenaviruses

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The disease potential for rodent-borne agents is vast; its extent and magnitude are beginning to be understood for only a few groups of agents. One group for which great recent progress has been made is the rodent-borne haemorrhagic fevers, caused by the hantaviruses and arenaviruses. I will use these two families to illustrate the potential diversity of zoonotic agents, as well as the methodologies and the value of ecological studies of rodent reservoirs for zoonotic diseases.

The hantaviruses and arenaviruses, although not closely related taxonomically, have a number of important characteristics in common. Each virus is associated with a specific rodent host of the family Muridae in which it establishes a chronic, generally asymptomatic infection involving the shedding of virus into the environment. Humans become infected via inhalation of aerosolised virus. The haemorrhagic fevers caused by these viruses in humans cause significant morbidity (e.g. perhaps 200,000 cases of haemorrhagic fever with renal syndrome each year in China) and mortality (e.g. up to 50% of cases of hantavirus pulmonary syndrome [HPS] may be fatal in the Americas). The number of recognised agents in these two groups has undergone an exponential expansion in recent years. Despite their recent discovery, evidence suggests that these agents have coevolved in association with their rodent hosts for millions of years; and these coevolutionary patterns suggest that there may be many additional specific host/virus associations which remain to be discovered.

Recently, intensive ecological studies have provided important insight into the natural history of the rodent reservoirs for several haemorrhagic fever viruses. A combination of intensive cross-sectional and longitudinal studies has examined reservoir distribution and population dynamics, and the prevalence and incidence of infection in reservoir populations. These studies provide data which allow the identification of specific times and places of increased risk of human disease and suggest specific mechanisms by which public health officials might intervene in order to minimise the incidence of human disease.

ORAL PRESENTATIONS

Rodent-borne *Bartonella*: their importance to human health

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The genus *Bartonella* (family Bartonellaceae) consists of gram-negative bacteria that are frequently haemotrophic parasites of the red blood cells of various vertebrates, including humans. *Bartonella* cause several important diseases, including cat scratch disease (*B. henselae*), trench fever (*B. quintana*), bartonellosis (*B. bacilliformis*), and endocarditis (*B. elizabethae*). Recognition of a wide range of clinical diseases in immunocompetent and immunocompromised humans caused by *Bartonella* species has provided the impetus for the identification of the vectors and nonhuman reservoirs of these bacteria.

Numerous species of *Bartonella* circulate in wild mammals, but our understanding of the natural history of any single species is incomplete. In the United States at least four unique genotypes of *Bartonella* have been shown to infect at least six species of native rodents. However, the importance of these *Bartonella* isolates in causing human disease is not established.

Bartonella isolated from blood samples of *Rattus rattus* and *R. norvegicus* captured in six States of the USA was examined. Primers producing a 379-bp amplicon of the citrate synthase gene (*gltA*) were used in the polymerase chain reaction (PCR). Nucleotide base sequence data were obtained on purified PCR products. Isolates were obtained from 65 of 323 *R. norvegicus* and 10 of 87 *R. rattus*. Infection in *R. norvegicus* was highly focal, ranging from 0% (0 of 87, New York; 0 of 35, Nevada) to 58% (36 of 62, Louisiana); overall prevalence was 21% (67 of 325). Isolates were most closely related to *B. elizabethae* by *gltA* sequence, ranging from identity to 93%. All rat isolates clustered in phylogenetic analyses with *B. grahamii* from *Clethrionomys glareolus* captured in the U.K. and with an isolate obtained from *Mus musculus* captured in the USA. These data support a hypothesis of an Old World origin for *Bartonella elizabethae*-like agents recovered from rodents introduced into the USA and South America. *Bartonella elizabethae* is a known human pathogen; these apparent rodent reservoir findings may have potential public health significance wherever Old World rats are found.

Studies on rodent transmitted diseases in Tanzania

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Rodents have been known for centuries to spread major diseases of humans and livestock. In some parts of the world, environmental and pest management systems have succeeded in keeping rodent populations at significantly low levels, such that rodents

no longer present a threat to health. In certain regions of the developing world, however, rodents continue to be a major public health hazard. In Tanzania, research is going on in selected areas to study the epidemiology of rodent-transmitted (zoonotic) diseases (plague, leptospirosis and murine typhus), alongside taxonomical and ecological studies of rodents. Recent research suggests that plague has been persistent in certain areas of Tanzania for almost two decades, and human cases are reported annually. Leptospirosis has been shown to be widespread amongst livestock and humans, and preliminary studies on the prevalence of murine typhus are being carried out to determine prevalence of this disease in the country. This paper reports briefly on these research activities and related findings.

A serological study for rat cytomegalovirus in rice field rats (*Rattus argentiventer*)

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A serological study for rat cytomegalovirus (RCMV) was conducted in five different geographic locations of Malaysia. Rice field rats (*Rattus argentiventer*) were captured using a live-capture method known as the trap-barrier system (TBS). Rats were sacrificed and blood was collected by cardiac puncture. An indirect enzyme-linked immunosorbent assay (ELISA) was developed to detect the presence of antibody against RCMV in rat sera. Results showed that more than 50% of 278 rat sera tested were strongly positive for RCMV, indicating significantly elevated antibody levels. The finding was found to be consistent in all geographical locations.

Further tests were conducted to determine serological cross reactivity between RCMVs of *Rattus norvegicus* and *Rattus argentiventer*. Both conventional and hyper-immune sera were used in an ELISA test. Results indicated that antibodies prepared against individual viruses were highly reactive against these heterologous antigens.

The sera collected in the field were also tested for the presence of antibodies against *Mycoplasma pulmonis* and other viruses, including rat coronavirus, adenovirus, new rat parvovirus, conventional parvovirus, Theiler's virus, lymphocytic choriomeningitis virus, vaccinia virus, Hantaan virus, Seoul virus, pneumonia virus and Sendai virus. The test used in this study was an indirect immunofluorescence and serum samples were scored as either positive or negative against the individual antigens. The results indicated that 36% and 13% of the samples were positive for mycoplasma and rat coronavirus, respectively. Less than 10% of the sera were positive for adenovirus, new rat parvovirus, conventional parvovirus and Theiler's virus. None of the serum samples tested was positive for lymphocytic choriomeningitis virus, vaccinia virus, Hantaan virus, Seoul virus,

pneumonia virus and Sendai virus. Our data imply that RCMVs are persistently and effectively maintained in the rice field rat populations. Compared with other viruses and mycoplasma, RCMV was found to have a high sero-prevalence within rat populations. It is suggested, therefore, that the virus could be manipulated for the development as a suitable biological vector to control rat population in rice fields.

Characterisation of new rat cytomegaloviruses isolated from rice field rats (*Rattus argentiventer*)

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Two different rat cytomegaloviruses (RCMV) were successfully isolated from the rice field rat. These viruses were individually isolated from the kidney and salivary glands of different individual rats. The rice field rats used for virus isolation were captured alive and examined to be clinically healthy. Rats were autopsied and individual organs of interest were collected and processed under a sterile environment for virus isolation. Individual tissue extracts were then co-cultured with rat embryo fibroblast.

Cytopathic effects, characterised by focal development of typical cytomegalovirus plaques, were observed within 4 to 6 days of co-culture. The presence of cytopathic effects was further visualised upon haematoxylin-eosin staining. Eosinophilic cytoplasmic and intranuclear inclusion bodies were observed under light microscope at higher magnifications. Typical morphology and size of the cytomegaloviruses were determined using transmission electron microscopy. The size and morphology of the viral particles were indistinguishable to those of an English strain of RCMV. An indirect immunoperoxidase test was used to further confirm the presence of RCMVs. Infected tissue strongly reacted against reference RCMV antisera. Polymerase chain reaction was employed in random amplified polymorphism DNA analysis to determine the relationship of the two virus isolates with the established RCMVs of the Dutch and English strains which were isolated from *Rattus norvegicus*. The results indicated that the two viruses isolated from the kidney and salivary gland of *Rattus argentiventer*, respectively, were RCMVs. The two isolates were found to be genetically different from each other but serologically closely related to the RCMV English strain.

Interrelationship of *Leishmania* parasites and rodents in arid regions of Asia

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Zoonotic cutaneous leishmaniasis (ZCL) is an obligate transmissible infection with natural focality. In a number of arid regions of Asia the disease is still a problem for

the public health services. In 1985 a detail review of regional geography of cutaneous leishmaniases in the Old World was published and features of distribution and ecology of different *Leishmania* (*L. major*, *L. tropica*, *L. gerbilli*, *L. ethiopica*, *L.* were described and relevant zonations of their nosoranges were presented. During recent sp.) years new data on natural focality of leishmaniases in Asia have been obtained, including a description of two new species (*L. arabica* and *L. turanica*). These discoveries have changed traditional notions considerably and should be taken into consideration by public health services. In the paper, the main results of studies of the *Leishmania* isolates from various natural foci of Mongolia, Uzbekistan, Turkmenistan and South of Kazakhstan are presented and compared with the data from other parts of Asian deserts. It is important to underline that only *L. major* is causing the ZCL morbidity among human beings, and it has different long-term fluctuations in different hypo-, meso-, and hyper-endemic foci; even within the overlapping zone of ranges of *Rhombomys opimus* (main host of three parasites species in Turan) and *Phlebotomus papatasi* (main vector of *L. major* in different parts of its nosorange) there are large areas with no risk of infection to people, but this situation could change if irrigation systems are developed. Pure *L. major* infection of wild rodents has not been found, and mixed infection (*L. major* + *L. turanica* or sometimes *L. major* + *L. turanica* + *L. gerbilli*) is typical for vast territories. Seasonal variations in *L. major* + *L. turanica* relative abundance have been detected both during a transmission season and in different years. If *L. turanica* could affect up to 100% of *R. opimus* population in many foci, *L. major* infection rate as a rule is not higher than 50% and even this level occurs only at the end of transmission season and in the most favourable habitats (river deltas and valleys, and piedmont areas).

Rodent-borne diseases and their control in China

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The earliest observations concerning rodent-borne diseases in China were recorded 5000 years ago. The diseases were plague and leptospirosis. Today, several rodent-borne diseases still occur. Cases of plague are rarely found, although natural epidemic foci exist and it still poses a threat. Haemorrhagic fever with renal syndrome (HFRS) requires major control because there are many epidemic foci and thousands of cases per year. Leptospirosis, with total cases fluctuating up and down, is partially transmitted by rodents. Other rodent-borne diseases, such as Lyme disease, are of serious concern but their epidemiology is not well understood.

There are at least 79 rodent species belonging to 12 families that are associated with the incidence of human diseases in China. About 10 species are the main hosts of the various zoonoses and so are the focus of control efforts. Rodent control on a large-scale produced good results for the control of rodent plague. However, the cost is high and the effect is short-lived, although the environment recovers. Currently, the strategy is to undertake surveillance and temporary control of the host rodent density. For HFRS, because there is now a highly effective vaccine for humans, the rodent

control measures include surveillance, focal point rodent control, and vaccination of highly susceptible people, and the disease foci are manageable. For leptospirosis, rodent control should be conducted only after it has been confirmed that rodents transmit this disease.

POSTER PRESENTATIONS

Norway rats, reservoir hosts for *Cryptosporidium parvum*

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Cryptosporidium parvum is a single-celled parasite which can cause severe gastrointestinal illness in both humans and livestock. The infection may be acquired by eating or drinking contaminated material. Commensal rodents, which appear to be asymptomatic carriers, may be a source of the contamination and Norway rats (*Rattus norvegicus*), in particular, may be an important vector. To determine this, populations of rats were studied on three infested sites, a livestock farm, the banks of a pond and its outflowing stream and a farm rubbish tip. Rats were regularly trapped, marked and released and a faecal sample was obtained from each animal. The parasite was detected in the sample by an immunofluorescence monoclonal antibody test. The study sought to quantify the rate of infection and how this varied with respect to rat population dynamics. Overall, the average rate of infection was 24.0% (n = 438), with no variation between the three sites. There was a significant weight (age) effect with 40.4% of juveniles (≤ 100 g body weight) infected, decreasing to 11.8% for rats over 400 g. More males were infected (28.8%) than females (19.2%). There was no strong evidence linking infection rate to population density. Seasonally, most infected rats were found in May–June (39.6%), the lowest number in September–October (13.0%). Radio-tagged rats had ranges that kept them in close to the farm buildings, pond or tip, thereby offering ample opportunity to pass on the infection. The results suggest that measures taken to reduce infection in cattle and clean-up water supplies should include rodent control, otherwise reinfection/recontamination will occur.

Symposium H

Rodents as Indicators of Environmental Change and Their Role in Maintenance of Ecosystem

PLENARY LECTURE

Rodent-ecosystem relationships: a review

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Because of their ability to use agricultural production and their role in spreading disease in humans, rodents are often viewed as having negative impacts in modified and natural ecosystems. Species that occur communally with humans, such as black, brown and Pacific rats and house mice, have acquired particularly notorious reputations. Some, such as the black rat, have been further implicated in the extinctions of many species of insular land birds and small mammals.

In this review, I focus on the interactions of rodents with chemical and structural attributes of the environment, and their direct and indirect impacts on food resources. Chemical interactions such as cycling of nitrogen and carbon can be affected markedly by the selectivity and intensity of rodent foraging. Peaks in mictotine rodents, for example, may direct flows of carbon and nitrogen from primary producers to the soil system, and reduce surface litter. Rates of mineralisation and fixation of nitrogen are affected. Effects of rodents on structural attributes of the environment are most obvious in 'ecosystem engineer' species such as beavers, prairie dogs and mole-rats. However, many rodents alter the structure of their environment more subtly by surface tunnelling, construction of leaf or stick nests, or even by arranging pebbles around tunnel entrances. The impoundments of North American beavers affect nutrient cycles, water and the species richness of aquatic invertebrates and fish; they also facilitate terrestrial leaf beetles by changing the chemistry of cottonwood host plants.

Facultative and obligate use of rodent burrows is also made by many species of vertebrates and invertebrates. Impacts of rodents on food resources vary from simple depletion of preferred food types to dramatic changes in the composition of prey communities. Impacts may be direct, as by foraging, or indirect, as by changing of soil structure, drainage and cycling of nutrients. Several species of arboreal rodents, primarily squirrels, have been implicated in the dispersal of tree seeds and mole-rats in the dispersal of geophytic plants; terrestrial rodents may disperse seeds via caching.

The foraging activities of rodents may facilitate other taxa such as ants and birds. Rodents appear to play a minor role in pollination in some systems and to effect dispersal of hypogean fungi that form mycorrhizal associations with plants. Although many of these interactions remain to be quantified, rodent-ecosystem relationships

are clearly diverse and often beneficial in terms of their effects on populations of other species. Understanding of rodent–ecosystem relationships is of considerable theoretical interest, and also essential if rodents are to have value as indicators of environmental change.

ORAL PRESENTATIONS

Rodents in disturbed forest habitats

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In the forests of Holarctic, newly disturbed areas constantly appear as the result of burning or clearcutting. Rodent communities characteristic of undamaged forest habitats disappear, and the areas are resettled by species from the neighbourhood. These new rodent communities are highly predominated by one species: in northern and central Europe it is usually *Clethrionomys glareolus* (although with some notable exceptions); in the northern part of Nearctic (northern U.S., Canada) by *Peromyscus maniculatus*, despite the fact that another *Clethrionomys* species (*C. gapperi*) is common in these habitats before the disturbance.

Why isn't *C. gapperi* in America equally successful in colonising the disturbed areas as *C. glareolus* in Europe? Published data have been analysed in order to gauge support for one (or more) of the following hypotheses and provide the answer to the above question:

1. *Peromyscus* is more suited to colonising such areas than is *Clethrionomys*. Absence of *Peromyscus* in Europe leaves the disturbed habitats free for *C. glareolus*.
2. *C. glareolus* is more generalistic and therefore better preadapted for resettling such areas than *C. gapperi*.
3. Historical duration of human management in forests affected breadth of niches of *Clethrionomys* species, and thus their ability to colonise disturbed areas.

Rodents as monitors of environmental contamination

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This paper is a summary of a research carried out during recent years in order to verify the suitability of using wild rodents to monitor the environmental impact of human activities and to assess the relationship between environmental pollution

and genotoxic damage. The work consists of the setting up of biological models, in particular a mammalian model, including sentinel species and relevant endpoints. Some rodent species (Rodentia, Muridae) were used as indicators for the following reasons: they are able to concentrate contaminants present in the ecosystem, they are easily trapped, readily available, characterised by a relatively small home range and a high reproductive rate.

Among the numerous endpoints for detecting biological damage, cytogenetic endpoints, observable in bone marrow and peripheral blood (micronuclei), and in sperm (abnormal sperm cells), were chosen. Two mutagenicity tests (micronucleus test and sperm abnormality assay) were applied on 893 rodents belonging to seven species: *Mus musculus domesticus* (n = 426), *Mus spretus* (n = 92), *Apodemus sylvaticus* (n = 64), *Apodemus flavicollis* (n = 35), *Rattus norvegicus* (n = 93), *Rattus rattus* (n = 37), and *Clethrionomys glareolus* (n = 146). Animals were collected in 24 differently contaminated sites, located in Italy, Sweden, Spain and the Czech Republic, to detect the possible genetic effects on resident populations. In some animal groups the contents of ¹³⁷-Cs and ¹³⁴-Cs and of heavy metals (lead, cadmium, zinc, copper) were analysed in total body and in target organs, respectively. Results showed that the frequency of micronucleated erythrocytes and abnormal sperm cells is significantly higher in rodents living in sites contaminated by radioactivity, petrochemical industry and in urban areas, in comparison with those sampled in areas characterised by negligible pollution. A significant correlation between radionuclide concentration and lead and cadmium content in soil and body and micronuclei frequency, was observed. The frequency of abnormal sperm cells and content of lead and cadmium were also significantly correlated. Furthermore the results show a different susceptibility among species. Whereas *A. sylvaticus* and *M. m. domesticus* seem suitable indicators because they are also able to assess the impact of the low level of pollutants, the usefulness of other species, such as *Rattus* spp. and *C. glareolus*, needs further investigation. Therefore the establishment of an international data bank to catalogue the species used in biomonitoring is proposed.

We propose that infesting rodents be used as sentinel species, whether in urban or agricultural environment. It would allow us to save rodents which, using the current disinfestation methods, would be eliminated. So, the use of these animals as monitors might also induce us to set up non-invasive methods for rodent control. These methods may be used in parallel and, where and when possible, to replace rodenticides. On the basis of these results, the possibility of including wild rodents in biomonitoring, not only in contaminated areas, but also in natural areas, which may become contaminated, is suggested in order to prevent risk.

The impact of rodents on forest regeneration in the mountain areas of Beijing, China

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From 1993 to 1995, the impact of rodents on forest regeneration in the mountain areas of Beijing was studied. The study aimed to assess the predation pressure on the seed bank by rodents, to find an effective method for reducing seed loss by rodents and to increase seed germination. The primary results are described briefly.

Rodents removed most of the oak, apricot and walnut seeds from the soil surface. When the seeds were protected by wire mesh, 23% of oak seeds and 24% apricot seeds on the soil surface germinated in the next year. Although the walnut seeds protected by the wire mesh were intact, none were observed to germinate. It seems that walnut seeds need more than one year to germinate. When seeds were sown about 5 cm deep into the soil, many of them survived. Oak seeds (39%) and apricot seeds (18%) germinated in the next year. We suggest that rodents play a very important role in forest regeneration in the mountain areas in Beijing. There is high potential for forest regeneration if seed loss is reduced. Sowing seeds under the soil may be effective in reducing seed loss by rodents and also in facilitating seed germination.

POSTER PRESENTATIONS

Rodent diversity in Vietnam

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The rodents of Vietnam are diverse and abundant. There are 64 species recorded which belong to 27 genera and 7 families. The taxonomy of rodents in Vietnam was revised using anatomical and cytological data. Chromosomal and DNA characteristics were reviewed for the genus *Rattus*.

This analysis provides a zoogeographical division of Vietnamese rodents and the distribution of species by latitude and habitat. Several species were determined to be threatened with extinction including *Rattus bicolor*, *Rattus affinis*, *Petaurista petaurista*, *Petaurista elegans*, *Hylopetes spp.*, *Belomys pearsoni* and *Callosciurus finlaysoni*.

The species of northern Vietnam include *Rhizomys sinensis*, *Dremomys pernyi*, *Callosciurus erythraeus*, *Rattus flavipectus*, *Niviventer bickit* and *Niviventer confucianus*. The species of southern Vietnam include *Hylopetes lepidus*, *H. spadiceus*, *Manetes berdmorei*, *Rattus exulans*, *Ratufa affinis*, *Callosciurus notatus*, *Callosciurus nigrovittatus* and *Scundasciurus hippirus*.

Microhabitat preferences of desert rodents in the southern Dzungaria Basin

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From March 1997 to June 1998, we investigated the five main microhabitat types in the southern Dzungaria Basin of Xinjiang China. These microhabitats can be classified according to the characteristics of terrain and vegetation: Type I, sand dune; Type II, valley between sand dunes associated with high perennial shrub (height>1.0m); Type III, flatland along the sand dune associated with herb and small perennial shrub (height<1.0m); Type IV, sand dune with perennial shrub; Type V, wash zone.

The results of our survey were as follows.

1. There were four rodent species observed in these microhabitats. *Rhombomys opimus* mainly inhabited Type III micro-habitat, *Meriones meriones meridianus* was in Type II, *Salpingotus crassicauda* was in Type IV and *Dipus sagitta* was found in all types.
2. The microhabitat uses of both bipedal rodents and quadrupedal rodents were correlated with the high perennial shrub (height > 1.0 m), although bipedal rodents preferred to move in open space while the quadrupedal rodents primarily foraged beneath the shrub. This result may be attributed to the risk of predation.
3. In the different seasons, *Dipus sagitta* shifted their microhabitat use between the different types. We believe this movement could be related to food supply.

Mechanisms of coexistence of desert rodent communities in the southern fringe of Dzungaria Basin

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This study was conducted in the southern part of Gurbantongout Sandy Desert, Fukang MAB Desert Ecology Station (87°45'–88°05'E, 43°50'–44°30'N) in 1996. Four rodent species were investigated, great gerbil, *Rhombomys opimus*, mid-day gerbil, *Meriones meridianus*, northern three-toed jerboa, *Dipus sagitta* and thick-tailed pygmy jerboa, *Salpingotus crassicauda*. The work aimed to study species diversity and reveal mechanisms of coexistence of rodent communities in the sandy desert. Phenological characteristics and food composition in the region were examined during two periods.

1. The rich ephemeral biomass period during April–June

Based on a three dimensional niche overlap, the habitat use was determined by spotlighting, the food by microscopic analysis of stomach contents and the time

by direct observations. Results indicated that, during April–June, each pair of the four rodent species had a high niche overlap and showed no significant ecological separation. This suggests that there is weak or no interspecific competition and they have a stable coexistence by using similar resources during this period.

2. Annual and perennial period during July–October

Great gerbil forage for shoots on bushes, forming a vertical resource separation with other species, enabling stable coexistence. The northern three-toed jerboa prefers open patches and forages as a gleaner, whereas the mid-day gerbil prefers bush patches and forages as a digger.

Using each species' population density, behaviour and the known available food, mechanisms of coexistence in the two periods were analysed. Firstly, during the ephemeral period given the abundance of food, space and the low population densities of all species, there was no competition. Also, we consider that two conditions must exist for this coexistence pattern. First, there is a restrained survival period in the rodent community that leads to a sharp decline in population size and second there is a rapid increase in resources. This phenomenon possibly exists in other rodent communities in high latitudinal regions. During the annual and perennial period when food is scarce for all rodents (except the great gerbil), variations in foraging behaviour and efficiency due to morphology and physiology allow a stable interspecific trade-off. This results in lower levels of competition between species. All these conditions are necessary ecological separations that allow sympatric species to coexist during periods of poor survival and low resource availability in desert environments where such resources fluctuate severely from year to year.

The rodent fauna composition, distribution and degree of damage in the gully region of the Loess plateau

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Trapping and plug recovery methods were employed in this study to investigate the mammalian species composition, their distribution and variation in population density in the Gully Region on Loess Plateau. Biomass and daily food consumption were used to evaluate the degree of damage by all species of rodent.

Rodent species composition. In this region, there are 11 species, belonging to 2 orders, 4 families and 7 genera. Of these there are 10 species of the order Rodentia, including 4 species of hamster, *Myospalax fontanieri* (Milne-Edwards), *Cricetulus triton* (de Winton), *Cricetulus longicaudatus* (Milne-Edwards) and *Meriones meridianus* (Pallas); 5 species of mice and rats, *Rattus norvegicus* (Berkenhout), *Mus musculus* (Linnaeus), *Rattus niviventer sacer*, *Apodemus peninsulae* (Thomas) and *Apodemus agrarius* (Pallas); 1 species of squirrel, *Eutamias sibiricus* (Laxmann);

and 1 species of hare, *Ochotona daurica* (Pallas). Eight of these species are considered to be Palearctic mammals, and comprise 73% of the total number of the species, of which northern zone species are found to be the dominant forms. Of the remaining species, two are widely spread and one is distributed in the oriental region.

Rodent population density dynamics and distribution characteristics. The population densities vary in different seasons. The density of rodents increases rapidly from April to August, where it reaches its peak. Capture rates in the peak period are more than 4 times that in the low-density period. The relative distribution of rodents in different environment habitats is greater in farmland than in orchards, uncultivated slopes and forestland. Distribution in dry and sloped landscapes is greater than in trenches and valleys.

Degree and time of damage. The combinations of biomass, daily food consumption and capture rate can accurately reflect the degree of damage. The damage caused by rodents relative to other species is in the order (highest to lowest) *Myospalax fontanieri* (Milne-Edwards), *Meriones meridianus* (Pallas), *Cricetulus triton* (de Winton), *Cricetulus longicaudatus* (Milne-Edwards), *Rattus niviventer* (Sacer), *Eutamias sibiricus* (Laxmann), and *Mus musculus* (Linnaeus). The rodents cause the most serious damage to crops in June, August and September.

Natural enemies of rodents and their protection and utilisation in the Loess plateau of West Shanxi, China

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The resources available for the natural enemies of rodents in the Loess Plateau, the west range of Shanxi, China were investigated. Food habits and food consumption were measured and analysed. A series of studies was conducted on protection and utilisation of natural enemies by planting trees and grass and by improving the ecological environment.

1. Species of natural enemy

In the literature there are over 30 species which are natural enemies of rodents. During three years of investigation, 20 species of natural enemies that belonged to 3 classes, 4 orders and 7 families were recorded: Columbridae, Reptilia; Accipitridae and Falconidae, Falconiformes, Aves; Attaginidae, Strigiformes, Aves; Canidae, Felidae and Mustelidae, Carnivora, Mammalia. Among them, *Otus scops sticronotus*, *Falco cherrug milvipes* are new records for this area.

2. Food habits and food consumption

Rodents make up 64% of the diet of snakes, 60% of predatory birds, and 71% of small carnivores. The daily food consumption of small predatory birds, medium bird predators, small carnivores and snakes is 30 g, over 20 g, near 200 g and about 3 g, respectively.

3. Protection and utilisation of natural enemies

Key measures for protection and utilisation of the natural enemies of rodents are to increase the public's awareness by improving the ecological environment and stopping the use of acute rodenticides, so as to reduce secondary poisoning. After the implementation of these measures for natural enemies in a 13 km² area of Xixian, Shanxi, China, the numbers of natural enemies showed a tendency to recover. Therefore, protecting the natural enemies of rodents and their environments helps to eliminate rodents and is an important measure of integrated management.

Microhabitat use of *Salpingotus crassicauda* in the southern Dzungaria Basin

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Salpingotus crassicauda is a bipedal rodent that lives very successfully in sandy deserts. It is a very small animal (average weight = 6.0 g, n = 8), and is regarded as very rare in Dzungaria Basin of Xinjiang, China. From March 1997 to June of 1998, we investigated the use by *Salpingotus crassicauda* of five microhabitat types in sandy desert in southern Dzungaria Basin.

This study showed that their microhabitat use was mostly limited to areas along the sand dune associated with herbs and small shrubs. In this microhabitat, there was greater insect density than in any other microhabitat type. The annual activity cycle of *Salpingotus crassicauda* coincides with that of insects. We think that the food is one of the main causes for selection of the microhabitat. Their annual activity cycle is from May to the end of October and this cycle is the shortest among the four coexisting rodent species in the sandy desert. Small body size, the shorter cycle of annual activity and the use of a limited microhabitat are regarded as some of the reasons for the rarity of this species.

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