

VOLUME 109 SUPPLEMENT 1994

Parasitology

Supplement to Parasitology 1994

Parasites and behaviour

EDITED BY **M. V. K. SUKHDEO**

CO-ORDINATING EDITOR **L. H. CHAPPELL**

CAMBRIDGE UNIVERSITY PRESS

Subscriptions may be sent to any bookseller or subscription agent or direct to the publisher: Cambridge University Press, The Edinburgh Building, Shaftesbury Road, Cambridge CB2 2RU. Subscriptions in the USA, Canada and Mexico should be sent to Cambridge University Press, Journals Department, 40 West 20th Street, New York, NY 10011-4211. All orders must be accompanied by payment. The subscription price (excluding VAT) of volumes 108 and 109, 1994 is £240 (US \$460 in the USA, Canada and Mexico), payable in advance, for ten parts plus supplements; separate parts cost £22 or US \$41 each (plus postage). EU subscribers (outside the UK) who are not registered for VAT should add VAT at their country's rate. VAT registered subscribers should provide their VAT registration number. Japanese prices for institutions (including ASP delivery) are available from Kinokuniya Company Ltd, P.O. Box 55, Chitose, Tokyo. Second class postage paid at New York, NY and at additional mailing offices. POSTMASTER: send address changes in USA, Canada and Mexico to *Parasitology*, Cambridge University Press, 110 Midland Avenue, Port Chester, New York, NY 10573-4930.

• ISBN 0 521 48542 8

© Cambridge University Press 1994

The Pitt Building, Trumpington Street, Cambridge CB2 1RP
40 West 20th Street, New York, NY 10011-4211, USA
10 Stamford Road, Oakleigh, Melbourne 3166, Australia

Printed in Great Britain by the University Press, Cambridge

Parasitology

Volume 109 Supplement 1994

Parasites and behaviour

EDITED BY

M. V. K. SUKHDEO

CO-ORDINATING EDITOR

L. H. CHAPPELL

WITHDRAWN



Contents

<i>Preface</i>	S1	The ecology of host-finding behaviour and parasite transmission: past and future perspectives	S31
<i>List of contributions</i>	S2		
Behaviours in trematode cercariae that enhance parasite transmission: patterns and processes	S3		
Introduction	S3	Summary	S31
Behavioural adaptations independent on the presence of the host	S3	Introduction	S31
Localization in the “host-space”	S3	Fecundity	S31
Locomotion	S3	Costs of reproduction	S32
Response to stimuli	S4	r/K strategies	S34
Adaptive value of the responses	S5	Dispersal	S34
Localization in the “host-time”	S6	Host location	S35
Adaptive value	S7	Response to the environment	S35
Possibility of other selective pressures	S8	Response to the host’s active space	S36
Behavioural adaptations depending on the presence of the host	S8	Response to the host	S36
Localization of the host by the cercariae	S8	Conclusions	S36
Physical stimuli	S8	References	S37
Chemical stimuli	S9		
Localization of the cercariae by the host	S9	Optimal habitat selection by helminths within the host environment	S41
Conclusion	S10	Summary	S41
References	S11	Introduction	S41
		The approach	S42
Physiological analyses of host-finding behaviour in trematode cercariae: adaptations for transmission success	S15	Problems with the chemical attraction hypothesis	S43
Summary	S15	The third environment	S44
Introduction	S15	Optimal behaviours in a predictable world	S44
Long-survival – swimming behaviour and patterns of movement	S15	Future directions	S47
Dispersal and locating host habitats – responses to the host active space	S17	Sensory mechanisms	S48
Approach to the host – responses to the host active space	S19	Optimal behaviours	S50
Dark stimuli	S19	Conclusions	S51
Water turbulence and touch	S21	Acknowledgements	S52
Chemical gradients	S21	References	S52
Host contact – responses to the host	S22		
Species invading mammalian hosts	S22	Doubt and certainty about the pathways of invasive juvenile parasites inside hosts	S57
Chemical host signals	S23	Summary	S57
Thermal gradients	S24	Introduction	S57
Adaptations to environmental conditions	S24	Blood transport: the building of a factoid	S57
Species invading birds	S24	Inductive reasoning: the generalization of a factoid	S58
Species invading fish	S25	Sampling at autopsy	S58
Conclusion	S25	A traditional procedure	S58
Acknowledgements	S26	‘Impedance’	S59
References	S26	Sampling in a perfect world	S59
		Sampling in the real world	S59
		A practical proof	S59
		Survey of previous data	S60
		Decisive experiments	S60
		Rival theories of migration of skin-penetrators	S60
		A unique opportunity	S61
		Proof in an enhanced experimental system	S61

An extended experimental framework	S62	More than two parasite species in the same host population	S99
‘Impedance’ redefined and the proof extended	S63	The population dynamics of the parasite community	S100
The proofs in context	S63	The effect of non-zero covariance	S100
Concluding comments	S64	A community with one host and five parasite species	S101
Acknowledgements	S65	Comparison with empirical data for helminth communities	S103
References	S65	Discussion	S105
Niche restriction in parasites: proximate and ultimate causes	S69	Acknowledgements	S107
Summary	S69	References	S107
Introduction	S69	The evolution of parasite manipulation of host behaviour: a theoretical analysis	S109
Results and discussion	S69	Summary	S109
Definition of niche	S69	Introduction	S109
Niche dimensions	S69	Optimal manipulative effort	S110
Methods to measure niche width	S69	Factors influencing the optimal manipulative effort	S111
Evidence for niche restriction	S70	Parasite infrapopulation size	S111
Causes for niche restriction and segregation	S71	Prevalence of parasite infections	S113
Proximate causes	S71	Parasite longevity inside the host	S114
Ultimate causes – saturation of niches with species	S74	Host longevity following infection	S114
Avoidance of interspecific competition	S77	Passive transmission rates	S115
Avoidance of predation	S78	Parasite fecundity	S115
Avoidance of hyperparasitism	S78	Discussion	S115
Facilitation of mating	S79	Acknowledgements	S117
Reinforcement of reproductive barriers	S80	References	S117
Adaptations to environmental complexity	S80	‡ Physiological bases for parasite-induced alterations of host behaviour	S119
Conclusion	S80	Summary	S119
Acknowledgements	S81	Behaviour and physiology	S119
References	S81	Parasitism and control systems	S120
Evolutionary factors influencing the nature of parasite specificity	S85	Neural	S120
Summary	S85	Behavioural neuromodulation	S120
Introduction	S85	Parasitism and neuromodulation of host behaviour	S120
Theoretical considerations	S85	Parasitism, endogenous opioid and immune systems	S121
Specificity and the origins of parasitism	S86	Endocrine	S125
Host-generated specificity	S87	Parasitism and host sex	S125
Specificity as an adaptation	S88	Parasitic castration	S127
Specificity and the mating imperative	S88	Effects of parasitism on developmental behaviour patterns	S128
Specificity and host-parasite coevolution	S88	Effects of parasite secretions on host behaviour	S128
Adaptation to host phenology	S88	Parasitism and the adaptiveness of behaviour: pathology and manipulation	S129
Hatching and excystment cues	S88	Conclusion	S131
Migration cues	S89	References	S131
Cell surface receptors	S89	‡ Behavioural defense against parasites: interaction with parasite invasiveness	S139
Immunological interactions	S90	Summary	S139
Specificity and the functional role of the host	S90		
Specificity and competition	S91		
Conclusions	S91		
Acknowledgements	S92		
References	S92		
The population dynamics of parasitic helminth communities	S97		
Summary	S97		
Introduction	S97		
Description of the model	S98		

Introduction	S139	Evasion of grooming by ticks	S146
Behavioural defenses against parasites	S141	Exploitation of grouping by ectoparasites and flies	S147
Grooming and ectoparasites	S141	Depression of fly-repelling behaviour	S148
Animal grouping and parasitic flies	S144	Counteracting selective foraging	S148
Fly-repelling behaviour	S145	Conclusion	S149
Foraging behaviour to avoid faecal-borne parasites	S145	Acknowledgements	S149
Evasion or exploitation of host behavioural defenses by parasites	S146	References	S149