

- 10 DeAngelis, D.L. (1992) *Dynamics and Nutrient Cycling, and Food Webs*, Chapman & Hall
- 11 Rosenzweig, M.L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171, 385–387
- 12 Polis, G.A. *et al.* (1996) Time, space, and life history: influences on food webs. In *Food Webs, Integration of Patterns and Dynamics* (Polis, G.A. and Winemiller, K.O., eds), pp. 435–460, Chapman & Hall
- 13 Yodzis, P. and Innes, S. (1992) Body size and consumer resource dynamics. *Am. Nat.* 139, 1151–1175
- 14 McCann, K. and Yodzis, P. (1995) Bifurcation structure of a three-species food chain model. *Theor. Popul. Biol.* 48, 93–125
- 15 Vannote, R.L. *et al.* (1980) The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37, 130–137
- 16 Odum, E.P. (1970) *Fundamentals of Ecology* (3rd edn), Saunders
- 17 Barnes, R.S.K. and Hughes, R.N. (1988) *An Introduction to Marine Ecology*, Blackwell
- 18 Barry, J.P. and Dayton, P.K. (1991) Physical heterogeneity and the organization of marine communities. In *Ecological Heterogeneity* (Kolasa, J. and Pickett, S.T., eds), pp. 270–320, Springer-Verlag
- 19 Murphy, G.I. (1981) Guano and the anchovetta fishery. *Res. Manag. Environ. Uncert.* 11, 81–106
- 20 Swap, R. *et al.* (1992) Saharan dust in the Amazon basin. *Tellus B* 44, 133–149
- 21 Vitousek, P.M. and Sanford, R.L., Jr (1986) Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17, 137–167
- 22 Drent, R.H. and Prins, H.H.T. (1987) The herbivore as a prisoner of its food supply. In *Disturbance in Grasslands* (vanandel, J. *et al.*, eds), pp. 131–148, Kluwer
- 23 Strong, D. (1992) Are trophic cascades all wet? Differentiation and donor control in species ecosystems. *Ecology* 73, 747–754
- 24 Lawton, J.H. (1989) Food webs. In *Ecological Concepts* (Cherrett, J.M., ed.), pp. 43–78, Blackwell
- 25 Vitousek, P.M. (1994) Beyond global warming: ecology and global change. *Ecology* 75, 1861–1876
- 26 Kitchell, J.F. *et al.* (1999) Nutrient cycling at the landscape scale: the role of diel foraging migrations by geese at the Bosque del Apache National Wildlife Refuge, New Mexico. *Limnol. Oceanogr.* 44, 828–836
- 27 van Eerden, M.R. *et al.* (1995) Riding on the crest of the wave: possibilities and limitations for a thriving population of migratory cormorants *Phalacrocorax carbo* in man-dominated wetlands. *Ardea* 83, 1–9
- 28 De Nie, H. (1995) Changes in the inland fish populations in Europe in relation to the increase of the cormorant *Phalacrocorax carbo sinensis*. *Ardea* 83, 115–122
- 29 Weseloh, D.V. *et al.* (1995) Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution and reproductive output between 1913 and 1991. *Colon. Waterbirds* 18 (Spec. Publ. 1), 48–59
- 30 Abraham, K.F. *et al.* (1996) Why are there so many white geese in North America? In *7th International Waterfowl Symposium* (Ratti, J.T., ed.), pp. 79–92, Ducks Unlimited
- 31 Ankney, C.D. (1996) An embarrassment of riches: too many geese. *J. Wildl. Manage.* 60, 217–223
- 32 Lanyon, L.E. (1995) Does nitrogen cycle? Changes in the spatial dynamics of nitrogen with industrial nitrogen fixation. *J. Prod. Agric.* 8, 70–78
- 33 Jefferies, R.L. (1999) Herbivores, nutrients and trophic cascades in terrestrial environments. In *Herbivores: Between Plants and Predators* (Olf, H. *et al.*, eds), pp. 301–330, Blackwell
- 34 Abraham, K.F. and Jefferies, R.L. (1997) High goose populations: causes, impacts and implications. In *Arctic Ecosystems in Peril* (Batt, B.D., ed.), pp. 7–72, US Fish and Wildlife Service and Canadian Wildlife Service
- 35 Bucher, E.H. (1990) The influences of changes in regional land-use patterns on *Zenaida* dove populations. In *Granivorous Birds in the Agricultural Landscape* (Pinowski, J. and Summer-Smith, J.D., eds), pp. 291–303, Proceedings of General Meetings of the Working Group on Granivorous Birds, INTERCOL
- 36 Post, D.M. *et al.* Prey preference by a top predator and the stability of linked food chains. *Ecology* (in press)
- 37 Pimm, S.L. and Lawton, J.H. (1978) On feeding on more than one trophic level. *Nature* 275, 542–544
- 38 Oksanen, L. (1991) Trophic levels and trophic dynamics: a consensus emerging? *Trends Ecol. Evol.* 6, 58–60

Cognitive ecology: a field of substance?

Sue Healy and Victoria Braithwaite

Seven years ago, the phrase ‘cognitive ecology’ was coined by Real¹. Although no strict specifications as to what this new field encompassed were provided, Real suggested that there was sufficient new integrative research for this label to be useful. We think it timely to review the support for this claim. There are those who will dispute the value of yet another label for yet another subdiscipline, and if little has happened in seven years such critics would be right. However, there are several recent examples that suggest that ‘cognitive ecology’ does exist, although the field is perhaps not as wide-ranging as put forward by Dukas². We define cognitive ecology as work that attempts to integrate functional explanations of behaviour, such as those provided by behavioural ecology, with an understanding of the

In 1993, Les Real invented the label ‘cognitive ecology’. This label was intended for work that brought cognitive science and behavioural ecology together. Real’s article stressed the importance of such an approach to the understanding of behaviour. At the end of a decade in which more interdisciplinary work on behaviour has been seen than for many years, it is time to assess whether cognitive ecology is a label describing an active field.

Sue Healy and Victoria Braithwaite are at the Division of Biological Sciences, King’s Buildings, University of Edinburgh, West Mains Road, Edinburgh, UK EH9 3JT (s.healy@ed.ac.uk; v.braithwaite@ed.ac.uk).

underlying psychological and neural mechanisms.

The past

By 1993, there were a sufficient number of experimental examples of animal cognition, directed at understanding naturally occurring, complex behaviours, to spawn cognitive ecology. For example, scatterhoarding songbirds like the marsh tit (*Parus palustris*) can store many hundreds of food items, accurately retrieving a substantial proportion of this food after a few hours or days³. Congeneric species, such as the great tit (*Parus major*), do not store food and therefore do not

seem to require this kind of memory capacity. Comparisons of the learning and memory abilities of these, and other storing and nonstoring, birds in the laboratory revealed some evidence supporting the prediction, based

on the variation in the species' natural history, that the storing species had the better spatial memory⁴. Similarly, the polygynous male meadow vole (*Microtus pennsylvanicus*), which expands its range during the breeding season to search for mates, has superior spatial abilities (in various laboratory tasks, such as solving mazes) compared with both the more sedentary female meadow vole, and the male and female prairie voles (*M. ochrogaster*) – a closely related monogamous species that does not undergo range expansion⁵.

Comparative analyses examining the relationship between specific neural substrates, which support various aspects of cognitive capacity were also undertaken around this time. For example, hippocampal volume (the hippocampus is the area of the brain playing a major role in processing spatial information) was shown to be significantly larger in food-storing songbirds than in nonstoring songbirds^{6,7}, and was also found to be larger in male polygynous voles than in conspecific females⁸. Based on a handful of such examples, and on a theoretical framework provided by Gallistel⁹, Real¹ proposed that functional explanations alone were unlikely to be sufficient for explaining behaviour (this was not the first time such a proposal had been made, for example, Guilford and Dawkins and receiver psychology¹⁰). Real¹ focused particularly on the need to understand animals' subjective representations of environmental patterns, specifically in time and in space. Of these two, the vast majority (in terms of the number of studies and the diversity of research) of the work since 1993 has focused on the use of spatial representations, and therefore we will largely restrict our discussion here to that aspect of Real's proposal.

The present

An important merit of cognitive ecology lies in its integrative approach. By tackling behaviour from more than one starting point, a greater insight into a range of behaviours, such as animal orientation, song learning, mate choice and foraging, as well as insights into the similarities between the psychological processes of animals and humans, is being achieved. For example, mathematical abilities are often regarded as human-specific features and yet, recently, Hauser *et al.*¹¹ found that rhesus monkeys (*Mucaca mulatta*) are capable of carrying out simple arithmetic operations and thus might use similar mathematical representations to those of human infants. More surprisingly, a basic geometrical skill might have been observed in birds. Kamil and Jones¹² showed that Clark's nutcrackers (*Nucifraga columbiana*) appear to perform line bisection in a way previously seen only in humans. These birds learned that food could be found halfway between two landmarks, irrespective of the distance between the landmarks. An even more fascinating finding has come from observing the general learning and memory abilities used during the natural cache retrieval behaviour of food-storing birds. In the past, it was claimed that humans differed from animals in terms of the content of their memories. This proposal has been difficult to dispute owing to the lack of a suitable animal model paradigm¹³. However, new work by Clayton and Dickinson¹⁴ found that scrub jays' (*Aphelocoma coerulescens*) memories resemble human episodic memories (the what, when and where of an event¹³). The scrub jays not only remembered what they had stored, and where it was hidden, but they could also remember when they had stored the food. All of this information was used to direct their cache retrieval behaviour. Realizing that monkeys and birds use cognitive processes akin to those of human learning and memory has been achieved because of the viewpoint provided by cognitive ecology, which encompasses both mechanistic and functional approaches.

Neural substrates of spatial memory

There has been a flurry of work on the role of spatial cognition and its neural substrates: more recent comparative analyses have shown that hippocampal volume is enlarged concomitantly with several behaviours that apparently require an increased demand for spatial memory: in nest-parasitic female cowbirds (*Molothrus ater*) and in males that help the female search for nests¹⁵; in migrant passerines but not in related resident species¹⁶; and in relation to the degree of food storing practised in a range of bird species^{17,18}. The greater size of the hippocampus in food storers appears to be caused, at least in part, by an increase in the number of neurons, not their density, and might be due to a combination of neurogenesis and inhibition of apoptosis (programmed cell death)¹⁹.

Comparative analyses also provide evidence for seasonal changes in hippocampal volume, appearing to match changes in demand for spatial memory^{20,21}. Although two assumptions are made implicitly in these studies (that the hippocampus is carrying out spatial computations and that it is costly to enlarge the hippocampus), only one of these correlations has been explored experimentally: Clayton and Krebs¹⁹ hand-raised marsh tits and showed that the experience of food storing is required to bring about hippocampal expansion. A knowledge of food-storing behaviour, developmental manipulation and the investigation of neural structural changes have together provided the first demonstration that specific behaviours do effect structural change in 'cognitive' regions of the brain. The next step is to clarify what cognitive advantages (e.g. increased duration of spatial information or increased storage capacity) are being provided by these structural changes. The high cost of enlargement is suggested by the evidence that, at least in part, experience-induced neurogenesis is required for expansion²².

Species differences in spatial cognition

Comparing hippocampal volumes of storing with nonstoring species was not only a novel and productive approach to understanding the relationship between behaviour and neuroscience, but also led to the collection of data on the cognitive advantages that are conveyed to animals with an enlarged hippocampus. Food-storing species are better than nonstoring species at tasks requiring spatial memory and they also pay more attention to spatial information than do nonstoring species^{23,24}. The assumption is that these kinds of psychological differences and advantages, gained from enlarging the hippocampus in food storers, will also be found in other species in response to other kinds of ecological spatial demands. This requires confirmation. The tasks used in the storer/nonstorer comparison to test these birds' learning and memory abilities combined typical psychological testing procedures with elements more akin to the animals' behaviour in the field. For example, in some experiments, birds were required to return to locations (e.g. on artificial trees in a laboratory) in which they had seen, but been unable to remove, food²³. The integration of tried and true psychological methods with testing animals in a semi-natural environment was informative in that instance and promises to be a useful model approach for investigating other instances in which differences in cognitive abilities are predicted from neural variation.

Although we do not know much about the neural processing of spatial information in fish, variation in spatial cognition in fish can be correlated with environmental predictability. Sticklebacks (*Gasterosteus aculeatus*) from stable environments (e.g. ponds) learn to swim through a maze faster if they can see visual landmarks, whereas fish from

Box 1. Orientation mechanisms

In 1978, O'Keefe and Nadel²⁹ proposed that the mammalian hippocampus was the region of the brain that enabled the construction and maintenance of a 'cognitive map' – a neural representation of the spatial layout of the animal's environment. On such a map, landmarks and places are defined relative to each other rather than relative to the animal's body and would allow the animal flexibility in navigational responses, such as taking short cuts, detours and heading towards hidden goals. Simpler mechanisms for orientation have also been proposed (indeed, many form the basis for the cognitive map⁴¹), including:

- Simple orienting responses to environmental stimuli (taxes and kineses).
- Dead reckoning (path integration), which allows an animal to determine its location from a record of its own movement.
- Piloting using the landmarks surrounding the goal.
- 'True' navigation, in which animals head to an unfamiliar goal (e.g. some migrants on their first trip) or are displaced to an unfamiliar release point (e.g. homing pigeons).

Box 2. Neural capacity and behavioural demand

The song system, with quantifiable parameters like song repertoire size, offers an opportunity to investigate how closely behavioural output matches neural capacity. Chew *et al.*⁴² showed that neurons in the zebra finch (*Taeniopygia guttata*) caudomedial neostriatum (NCM) are specifically responsive to many individual conspecific songs and calls, even though many of these are very similar. The neurons were far less responsive to the songs of other birds and artificial sounds. Conspecific song also induces expression of an immediate early gene, *zenk*, and protein synthesis blockade in the NCM soon after training blocks learning^{43,44}. At least some of the time, cognitive capabilities appear to match behavioural demands. For example, male hooded warblers (*Wilsonia citrina*), which return to former breeding territories after migration, remember the songs of neighbours from the previous year and the locations at which they had been sung⁴⁵. However, the song sparrow (*Melospiz melodia*) has a median repertoire size of eight songs, but can apparently discriminate between 64 different conspecific songs⁴⁶. The costs and benefits of possessing greater cognitive abilities than those required are not clear.

Box 3. Cognitive mechanisms for mate choice

There are many examples to support our case for the value of using a cognitive ecological approach to help understand mate choice (e.g. work investigating memory of an order of items experienced in rats, known as serial position curves⁴⁷, might offer insight for those who propose a role for spatial memory in mate searching⁴⁸). Not all of these examples are based on speculation. For example, 'peak shift' has been suggested as a mechanism underpinning female preference for males with elaborate characters⁴⁹. An animal that has learned to discriminate between a positive and a negative stimulus might later show a preference for stimuli with exaggerated positive characteristics – this is the peak shift phenomenon. It is possible that sexual imprinting could provide a situation in which young females might learn to discriminate between two stimuli in such a conditional fashion, thus resulting in females that prefer to mate with individuals appearing to be exaggerated versions of their father⁵⁰. Here, a well known psychological mechanism might be provided with an adaptive context although we are presented simultaneously with a way in which animals' choices can drive traits in a single direction.

less stable environments (e.g. rivers) appear not to need these landmarks²⁵. Such intraspecific variation provides the most convincing evidence of differences in cognitive abilities among animals because it becomes less probable that phylogenetic differences are sufficient to account for observed behavioural differences. Speed of learning also seems to be positively correlated with environmental variation^{26,27}.

The understanding of both food storing in birds and territoriality in fish has been enhanced by applying modified psychological testing techniques to investigations of behaviours seen in the field.

How do animals orient?

More generally than these instances of increased spatial demand, a cognitive ecological approach offers the way to

achieve a comprehensive understanding of how animals actually find their way around their environment. It has become clear over the past few years that animals have evolved a variety of orientation mechanisms²⁸. To understand the evolution and maintenance of this variation we need to know how ecological, psychological and neural variation fit together.

In some instances, insight into these mechanisms has come about by determining what the animals have to do to reach a destination. The cognitive map proposed by O'Keefe and Nadel²⁹ is an enticing possibility, but simpler alternative methods enable an animal to navigate reasonably successfully, without incurring the costs associated with acquiring, maintaining and using a cognitive map (Box 1). However, the simpler mechanisms are not without costs of their own: they are generally less flexible in terms of route planning and might produce spatial errors. Nevertheless, there are animals that have chosen an error-prone system rather than one requiring superior cognitive processing. For example, hamsters (*Mesocricetus auratus*) and some species of ant simply use path integration (i.e. dead reckoning) to return to previously learned feeding sites and to return home^{30,31}. Hamsters can do this using locomotor input alone, whereas wood ants (*Lasius fuliginosus*) constantly turn back to view their surroundings (i.e. taking 'snapshots')³².

Although hamsters and ants use different sensory inputs to operate their path integration systems they appear to have converged on similar navigating mechanisms. Is this because they have small brains or because a simple navigation mechanism allows sufficiently accurate navigation around the environments these animals live in? In other words, is the choice of navigation mechanism dependent on computational (i.e. neural) constraints, ecological constraints or both? These questions have yet to be addressed.

The future

Our understanding of birdsong is beginning to benefit from the cognitive ecology approach. Song learning and its neural bases have long been a profitable place to search for an understanding of how brain and behaviour fit together. However, by concentrating on one or two species such work soon focused on the neuroscience, leaving behind the behaviour. This was unfortunate given the impressive and unexplained variation that is associated with song. In addition, the evidence now suggests that the relationship between the song and the song nuclei of the brain is less clearcut than previously thought³³. However, comparative studies might offer a way to redress this balance. For example, Székely *et al.*³⁴ have shown that in European warblers (the Sylviidae) the part of the brain involved in song learning, the higher vocal centre (HVC), has a larger volume when birds have larger song repertoires. DeVoogd *et al.*³⁵ also found this was the case more widely across passerines.

Learning plays a major role in song development and in associated brain nuclei in males, but we do not know to what degree this experience induces structural changes in the different nuclei, in spite of the earlier claims to this effect³⁶ (Box 2).

Food storing, foraging, orientation and song learning are behaviours that perhaps were obvious candidates with which to epitomize the value of the integrative nature of cognitive ecology. Several other areas are ripe for such an approach. Mate choice and signalling are two of those which are currently receiving a great deal of attention from behavioural ecologists. It might be the case that females use male morphological and behavioural traits to assess their genetic value. However, we think that the effects of learning and perhaps subsequent experience on a female's

mate choice might well result in her choosing a different male from the one predicted from a 'good genes' argument. The imprinting research has shown what a major role early learning can play in mate choice in adulthood³⁷. By implication, a female's choice of mate is likely to be directly affected by the male morphological and behavioural characteristics she is exposed to during development (frequently her father's; Box 3). For example, she might learn from her father what is a 'good' song or what is an impressive tail length. In addition, to determine which male she should choose, we need to know how many males' attributes a female can recognize and remember so that she can make her choice between them.

Cognitive ecology: substance or irrelevance?

In the seven years since Real's 1993 perspective, cognitive ecology has provided insight into our understanding of behaviour; it has revealed things that we did not know, elaborated some things that we already knew and pointed to intriguing problems for us to address in the future. In the next half decade there are going to be easy pickings for those who bridge the chasm (from either direction) between the investigations into mechanistic processes (the current domain of psychologists and neuroscientists working in laboratories) and the research based on functional explanations (the domain of behavioural ecologists often working in the field). Some of the most obvious of these morsels should be found in research into mate choice. More generally, signalling will also benefit from such an approach. It is already benefitting from investigations into the role that sensory processing plays in signal design and reception^{38,39}. Learning a new terminology and developing appropriate laboratory testing methods will be required, as will devising ways to take the laboratory out to the field⁴⁰. It will take more effort to make great strides in those areas in which cognitive ecology has already made itself felt, but even here the integrative approach that characterizes cognitive ecology should provide the most productive way forward.

Acknowledgements

We thank Melissa Bateson, Robert Biegler, Andy Hurly, Alex Kacelnik, Anthony McGregor, Sean Nee, Kate Oddie, Candy Rowe and Stewart West for helpful discussion. This article was written with support from grants to S.H. from BBSRC and Wellcome and to V.B. from NERC and The Royal Society.

References

1 Real, L.A. (1993) Toward a cognitive ecology. *Trends Ecol. Evol.* 8, 413-417
 2 Dukas, R., ed. (1998) *Cognitive Ecology*, The University of Chicago Press
 3 Cowie, R.J. et al. (1981) Food storing by marsh tits. *Anim. Behav.* 29, 1252-1259
 4 Krebs, J.R. et al. (1990) Spatial memory of Paridae: comparison of a storing and a non-storing species, the coal tit *Parus ater*, and the great tit, *P. major*. *Anim. Behav.* 39, 1127-1137
 5 Gaulin, S.J.C. and Fitzgerald, R.W. (1989) Sexual selection for spatial-learning ability. *Anim. Behav.* 37, 322-331
 6 Krebs, J.R. et al. (1989) Hippocampal specialization of food-storing birds. *Proc. Natl Acad. Sci. U. S. A.* 86, 1388-1392
 7 Sherry, D.F. et al. (1989) The hippocampal complex of food-storing birds. *Brain Behav. Evol.* 34, 308-317
 8 Jacobs, L.F. et al. (1990) Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proc. Natl Acad. Sci. U. S. A.* 87, 6349-6352
 9 Gallistel, C.R. (1990) *The Organization of Learning*, The MIT Press
 10 Guilford, T. and Dawkins, M.S. (1991) Receiver psychology and the evolution of animal signals. *Anim. Behav.* 42, 1-14
 11 Hauser, M.D. et al. (1996) Numerical representations in primates. *Proc. Natl Acad. Sci. U. S. A.* 93, 1514-1517

12 Kamil, A.J. and Jones, J.J. (1997) The seed-storing corvid Clark's nutcracker learns geometric relationships among landmarks. *Nature* 390, 276-279
 13 Griffiths, D. et al. (1999) Episodic memory: what can animals remember about their past? *Trends Cognit. Sci.* 3, 74-80
 14 Clayton, N.S. and Dickinson, A. (1998) Episodic-like memory during cache recovery by scrub jays. *Nature* 395, 272-274
 15 Reboreda, J.C. et al. (1996) Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *NeuroReport* 7, 505-508
 16 Healy, S.D. et al. (1996) Hippocampal volume in migrating and non-migrating warblers: effects of age and experience. *Behav. Brain Res.* 81, 61-68
 17 Healy, S.D. and Krebs, J.R. (1992) Food storing and the hippocampus in corvids: amount and size are correlated. *Proc. R. Soc. London Ser. B* 248, 241-245
 18 Hampton, R.R. et al. (1995) Hippocampal volume and food-storing behavior are related in Parids. *Brain Behav. Evol.* 45, 54-61
 19 Clayton, N.S. and Krebs, J.R. (1994) Hippocampal growth and attrition in birds affected by experience. *Proc. Natl Acad. Sci. U. S. A.* 91, 7410-7414
 20 Clayton, N.S. et al. (1997) Seasonal changes of hippocampus volume in parasitic cowbirds. *Behav. Proc.* 41, 237-243
 21 Smulders, T.V. et al. (1995) Seasonal variation in hippocampal volume in a food-storing bird, the black-capped chickadee. *J. Neurobiol.* 27, 15-25
 22 Patel, S.N. et al. (1997) Spatial learning induces neurogenesis in the avian brain. *Behav. Brain Res.* 89, 115-128
 23 Brodbeck, D.R. (1994) Memory for spatial and local cues: a comparison of a storing and a nonstoring species. *Anim. Learn. Behav.* 22, 119-133
 24 Hampton, R.R. and Shettleworth, S.J. (1996) Hippocampus and memory in a food-storing and a nonstoring bird species. *Behav. Neurosci.* 10, 946-964
 25 Girvan, J.R. and Braithwaite, V.A. (1998) Population differences in spatial learning in three-spined sticklebacks. *Proc. R. Soc. London Ser. B* 265, 913-918
 26 Mackney, P.A. and Hughes, R.N. (1995) Foraging behaviour and memory window in sticklebacks. *Behaviour* 132, 1241-1253
 27 Micheli, F. (1997) Effects of experience on crab foraging in a mobile and a sedentary species. *Anim. Behav.* 53, 1149-1159
 28 Healy, S.D., ed. (1998) *Spatial Representation in Animals*, Oxford University Press
 29 O'Keefe, J. and Nadel, L. (1978) *The Hippocampus as a Cognitive Map*, Oxford University Press
 30 Etienne, A.S. et al. (1998) Navigation through vector addition. *Nature* 396, 161-164
 31 Collett, M. et al. (1998) Local and global vectors in desert ant navigation. *Nature* 394, 269-272
 32 Judd, S.P.D. and Collett, T.S. (1998) Multiple stored views and landmark guidance in ants. *Nature* 392, 710-714
 33 Brenowitz, E. et al. (1991) Seasonal changes in avian song nuclei without seasonal changes in song repertoire. *J. Neurosci.* 11, 1367-1374
 34 Székely, T. et al. (1996) Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae). *Proc. R. Soc. London Ser. B* 263, 607-610
 35 DeVoogd, T.J. et al. (1993) Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses amongst oscine birds. *Proc. R. Soc. London Ser. B* 254, 75-82
 36 Gahr, M. et al. (1998) Sex difference in the size of the neural song control regions in a duetting songbird with similar song repertoire size of males and females. *J. Neurosci.* 18, 1124-1131
 37 Irwin, D.E. and Price, T. (1999) Sexual imprinting, learning and speciation. *Heredity* 82, 347-354
 38 Endler, J.A. (1998) Sensory ecology, receiver biases and sexual selection. *Trends Ecol. Evol.* 13, 415-420
 39 Ryan, M.J. (1990) Sexual selection, sensory systems, and sensory exploitation. *Oxford Surv. Evol. Biol.* 7, 157-195
 40 Healy, S.D. and Hurly, T.A. (1998) Hummingbirds' memory for flowers: patterns or actual spatial locations? *J. Exp. Psych. Anim. Behav. Proc.* 24, 1-9
 41 Dyer, F.C. (1998) Cognitive ecology of navigation. In *Cognitive Ecology* (Dukas, R., ed.) University of Chicago Press
 42 Chew, S.J. et al. (1996) A large-capacity memory system that recognizes the calls and songs of individual birds. *Proc. Natl Acad. Sci. U. S. A.* 93, 1950-1955

- 43 Mello, C.V. and Ribeiro, S. (1998) ZENK protein regulation by song in the brain of songbirds. *J. Comp. Neurol.* 393, 426–438
- 44 Mello, C. *et al.* (1995) Repeated exposure to one song leads to a rapid and persistent decline in an immediate-early genes response to that song in zebra finch telencephalon. *J. Neurosci.* 15, 6919–6925
- 45 Godard, R. (1991) Long-term memory of individual neighbours in a migratory songbird. *Nature* 350, 228–229
- 46 Stoddard, P.K. *et al.* (1992) Memory does not constrain individual recognition in a bird with song repertoires. *Behaviour* 122, 274–287
- 47 Kesner, R.P. *et al.* (1984) Serial-position curves in rats: order memory for episodic spatial events. *Anim. Learn. Behav.* 12, 378–382
- 48 Schwagmeyer, P.L. (1994) Competitive mate searching in thirteen-lined ground squirrels (Mammalia, Sciuridae): potential roles of spatial memory. *Ethology* 98, 265–276
- 49 Weary, D.M. *et al.* (1993) A product of discriminative learning may lead to female preferences for elaborate males. *Evolution* 47, 333–336
- 50 Vos, D.R. (1995) The role of sexual imprinting for sex recognition in zebra finches: a difference between males and females. *Anim. Behav.* 50, 645–653

CORRESPONDENCE

Brood parasitism: ducks can be cuckoos too

There are several omissions in the recent *TREE* review article by Winfree¹. For example, she did not mention that parasitism by the giant cowbird (*Scaphidura oryzivora*) is actually advantageous in *Oropendolas* spp. because the young cowbirds remove botfly larvae (from the genus *Philornis*) from the host's young, thus reducing their mortality². In addition, intraspecific brood parasitism in Anseriformes (which is much more common than the single case entered into Table 1) was not discussed³.

Parasites might benefit from intraspecific brood parasitism because the dispersal of eggs into more than one nest could potentially reduce the possibility of a female experiencing a single failed clutch⁴. Because predation and environmentally linked clutch losses are highest among hole-nesting precocial Anatidae, brood parasitism in this family is not considered surprising³. It has also been suggested that parasitic female wood ducks (*Aix sponsa*) benefit from parasitism when they are unable to locate suitable nest cavities⁵.

Intraspecific brood parasitism can also entail costs, including the increased time spent by the parasite away from their own nests while searching, which often results in the parasites themselves being parasitized by other individuals⁴.

Although it is usually assumed that avian brood parasitism is overwhelmingly disadvantageous to the host, this assumption is probably more relevant for altricial birds rather than for precocial birds because of the extra time and energy required to rear parasitic young (D.J. Towers, MSc thesis, University of the Waikato, New Zealand, 1990).

V. Benno Meyer-Rochow

Dept of Biology, Oulu University, SF-90570 Oulu, Finland (vmr@cc.oulu.fi)

References

- 1 Winfree, R. (1999) Cuckoos, cowbirds and the persistence of brood parasitism. *Trends Ecol. Evol.* 14, 338–343
- 2 Smith, N.G. (1968) The advantage of being parasitized. *Nature* 219, 690–694
- 3 Yom-Tov, Y. (1980) Intraspecific nest parasitism in birds. *Biol. Rev. Camb. Philos. Soc.* 55, 93–108
- 4 Brown, C.R. and Brown, M.B. (1989) Behavioural dynamics of intraspecific brood

parasitism in colonial cliff swallows. *Anim. Behav.* 37, 777–796

- 5 Semel, B. *et al.* (1988) Effects of brood parasitism and nest box placement on wood duck breeding ecology. *Condor* 90, 920–930

Reply from R. Winfree

For reasons of space, my recent *TREE* review article¹ was limited to obligatory interspecific brood parasitism. As Meyer-Rochow points out, intraspecific parasitism is a different phenomenon and will probably have different dynamics². For example, in extending the cost-benefit approach to the intraspecific case, the net effect of parasitism on both the host and the parasite has to be considered, because it is no longer true that the parasite is unable to raise its own young. One possible result of this is that the fitness of parasitic behavior within a species becomes frequency-dependent³.

Regarding anatids and precocity, the question is: why is facultative, intraspecific parasitism common among precocial species (91.5% of 117 species studied)⁴ and obligatory, interspecific parasitism uncommon (1 of 968 existing species, or 0.1%)^{5,6,7}, whereas the reverse is true for altricial species, with intraspecific parasitism being comparatively rare (32.7% of 101 species studied)⁴ and obligatory interspecific parasitism relatively common (92 of 8272 existing species, or 1.1%)^{5,6,7}.

I do not know the answer to this question, but several factors might contribute to these differences. First, relative to altricial species, precocial species provide little parental care, lowering both the host's cost of parasitism and the parasite's benefit from it^{8,9}. Second, precocial species lay relatively 'costly' eggs, which presumably increases the cost to the parasite of unsuccessful parasitism⁹. Third, because precocial species have larger clutch sizes, marginal analysis suggests that the percent benefit of laying an extra (parasitic) egg is less for precocial species¹⁰. Lyon and Eadie¹⁰ provide a clear formulation of these costs from the parasite's point of view. Finally, a more thorough investigation of this subject would need to count the number of precocial and altricial species more carefully (I excluded some groups which were not clearly in either category) and also to correct for phylogenetic non-independence.

Like Meyer-Rochow, I find Smith's¹¹ example of beneficial parasitism interesting. However, I didn't discuss it in my review because later studies in other parts of the giant cowbird's range^{12,13} haven't been consistent with parasitism being beneficial, thus it seems unlikely that this is one of the main forces allowing parasitism to persist.

Rachael Winfree

Dept of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA (rwinfree@princeton.edu)

References

- 1 Winfree, R. (1999) Cuckoos, cowbirds and the persistence of brood parasitism. *Trends Ecol. Evol.* 14, 338–343
- 2 Petrie, M. and Moller, A.P. (1991) Laying eggs in others' nests: intraspecific brood parasitism in birds. *Trends Ecol. Evol.* 6, 315–320
- 3 May, R.M. *et al.* (1991) Could intraspecific brood parasitism cause population cycles? In *Proceedings of the 20th International Ornithological Congress* (Bell, B.D. *et al.*, eds), pp. 1012–1022, Ornithological Trust Board
- 4 Rohwer, F.C. and Freeman, S. (1989) The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* 67, 239–253
- 5 Brooke, M. de L. (1991) A survey of modern birds. In *The Cambridge Encyclopedia of Ornithology* (Brooke, M. de L. and Birkhead, T., eds), pp. 85–120, Cambridge University Press
- 6 Nice, M.M. (1962) Development of behavior in precocial birds. *Trans. Linn. Soc. New York*, 20–21
- 7 Payne, R. (1997) Avian brood parasitism. In *Host-Parasite Evolution: General Principles and Avian Models* (Clayton, D.H. and Moore, J., eds), pp. 338–369, Oxford University Press
- 8 Sorenson, M.D. (1992) Why is conspecific nest parasitism more frequent in waterfowl than in other birds? *Can. J. Zool.* 70, 1856–1858
- 9 Rohwer, F.C. and Freeman, S. (1992) Why is conspecific nest parasitism more frequent in waterfowl than in other birds: a reply to M.D. Sorenson. *Can. J. Zool.* 70, 1859–1860
- 10 Lyon, B. and Eadie, J.M. (1991) Mode of development and interspecific avian brood parasitism. *Behav. Ecol.* 2, 309–318
- 11 Smith, N.G. (1968) The advantage of being parasitized. *Nature* 219, 690–694
- 12 Robinson, S.K. (1988) Foraging ecology and host relationships of giant cowbirds in southeastern Peru. *Wilson Bull.* 100, 224–235
- 13 Webster, M.S. (1994) Interspecific brood parasitism of *Montezuma oropendolas* by giant cowbirds: parasitism or mutualism. *Condor* 96, 794–798