Genetically engineered monogamy in voles lends credence to the modus operandi of behavioural ecology

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Behavioural ecologists investigate the evolutionary forces that select for one behavioural pattern over another (Krebs and Davies 1991, 1993.) Why do lions hunt in prides while the tiger stalks its prey alone? Why are honey bee workers so industrious while the drones are so lazy? Why do koels lay their eggs in the nests of crows while the latter go through the trouble of building nests and caring for chicks, their own as well those of the koel? Why do Siberian cranes fly some 6400 kilometres from their breeding grounds in Siberia to over winter in Bharatpur in Rajasthan, India, only to return to Siberia in summer? Why are males in many species of birds monogamous, pairing for life and providing paternal care to the chicks, while the males of many mammals are polygynous, mating with many females and contributing little more than a sperm-full of genes to their offspring?

Behavioural ecologists estimate, and wherever possible calculate, the relative costs and benefits of alternative behavioural strategies under the given ecological circumstances and attempt to predict the winning strategy. What are the relative advantages of cooperative hunting versus stalking in stealth, for the lion that lives in open savannas and the tiger that lives in dense jungle? What are the inclusive fitness benefits to the worker bee who rears sisters related to her by 0.75 instead of daughters related to her by 0.5, as compared to similar benefits for drones, of rearing sisters related to them by 0.5 instead of daughters related to them by 1.0? What are the benefits to the koel of saving the cost of nest building and brood care and to the crow of attempting to selectively destroy the koels' eggs without destroying her own? What are the costs for the Siberian crane of attempting to survive, let alone breed, in the severe winters of Siberia compared to the cost of risky and energy-consuming flights to Bharatpur and back? What are the costs to males of denying paternal care to their offspring when the mothers are up to the task by themselves and what are the costs to the females of abandoning their offspring?

Difficult as it is to do, these costs and benefits are often measurable. The more risky gambit of the behavioural ecologists appears to be the assumption that alternative behavioural strategies are readily available or easily created by mutation so that natural selection can choose from among them (Grafen 1991). The source of uncertainty is our profound ignorance of the proximate physiological, genetic or epigenetic, neurobiological and developmental mechanisms that orchestrate these behaviours. This ignorance has to do, in part but only in part, with the formidable difficulty of unraveling the proximate mechanisms of complex behaviour patterns. The remaining part has undoubtedly to be attributed to the behavioural ecologists' obsession with ultimate factors and habitual neglect of proximate causation (Gadagkar 1997).

But of course there are exceptions, and a particularly spectacular exception concerns our present understanding of the proximate factors involved in the presence and absence of affiliation, pair-bonding and paternal behaviour in voles. Voles are small mouse like rodents that can sometimes be serious pests. Of particular interest for this tale are two North American species, the prairie vole, Microtus ochrogaster, and the meadow vole, Microtus pennsylvanicus. These two species have contrasting mating systems. The prairie vole is very social, forms lasting pair bonds, males prefer the company of their mates and are aggressive to other individuals, and both parents provide extended parental care to offspring. In contrast, the meadow vole is rather asocial, mating is polygynous or promiscuous, mated pairs do not pair-bond and males do not provide parental care to offspring. There are also two other similarly contrasting species, the monogamous pine vole (Microtus pinetorum) and the promiscuous montane vole (Microtus montanus) which have been substituted for prairie voles and meadow voles, respectively, in some of the studies. Despite such contrasting social behaviour, prairie/pine voles and meadow/montane voles share more than 99% genome homology and look very similar. The obvious advantage of these vole species as model systems to investigate the evolution of social behaviour in general, and mating systems in particular, have

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long been recognized. Fortunately these contrasting behav-
ioral patterns are also seen in the laboratory, so that simple behav-
ioral assays involving preference for mates versus stran-
gers, affiliative behaviour and time spent huddling with mated partners, have been developed and used to quantita-
tively assess behaviour patterns under experimental condi-
tions.

A great deal is now known about the neuroendocrine modu-
lation of social and sexual behaviour of vertebrates in gen-
eral and mammals in particular. In mammals, two neu-
ropeptides, oxytocin and vasopressin, secreted by the hypo-
thalamus, are being increasingly implicated in a vari-
ety of socio-sexual behaviours. Oxytocin and vasopressin
are peptides with nine amino acids each and differ from
each other only in two amino acids. Oxytocin is associated
with female behaviours while vasopressin is associated with
those of the male. The monogamous prairie vole and the
polygynous meadow/montane voles have strikingly differ-
ent spatial patterns of expression of oxytocin and vasopressin
receptors in their brains. Not surprisingly, several investi-
gators including Thomas R. Insel, Larry J. Young, Zuoxin
Wang and their colleagues in Emory University in Georgia
(USA) have pursued the bold hypothesis of a causal rela-
tionship between the spatial patterns of action of oxytocin
and vasopressin and socio-sexual behaviour. The greatest
interest is in the differences between the monogamous, pair-
bonding, paternal prairie/pine male voles and the non-mo-
ogamous, non-pair-bonding, non-paternal meadow/ 
montane vole males, and most attention has been focused
on a class of vasopressin receptors called V1a (Young et al.
1998). V1a receptors are present in higher amounts in the
ventral forebrain in males of the monogamous species as
compared to the promiscuous species (Insel et al. 1994)
and this has been shown to be due to differences in gene
expression (Young et al. 1997). This difference has been
traced also to differences in gene sequences; the coding re-
gion of the gene for V1a receptor is highly (99%) conserved
in monogamous and promiscuous species. However, in the
monogamous prairie vole but not in the promiscuous
meadow vole, there is 428 bp, unstable, microsatellite DNA
element in the 5’ flanking, promoter region of the receptor
gene (Hammock and Young 2002). Nevertheless all this evi-
dence remains merely correlational and therefore not con-
clusive.

Several lines of direct experimental evidence have also
been brought to bear on this question. Intra-
cerebroventricular injection of an antagonist of the V1a
receptor into male prairie voles abolished their aggression
towards strangers and their preference for their mates, clearly
showing the role of vasopressin and its V1a receptor in bring-
ing about this species-specific behaviour (Winslow et al.
1993). More convincing is the experimental result that
transgenic mice which are otherwise hardly monogamous,
now affiliate significantly more with their mated partners
(Young et al. 1999). More recently, a novel adeno-associ-
ated viral vector has been employed to deliver the V1a
receptor gene to male mice, male prairie voles as well as to
males of the promiscuous meadow voles. The mice so treated
become more social as compared to controls (Landgraf et
al. 2003) and the male prairie voles become more affiliative
and show stronger preference for their mated partners
(Pitkow et al. 2001). The clinching evidence however comes
from the normally promiscuous male meadow voles receiv-
ing the V1a receptor gene from the monogamous prairie
voles, who now show significantly higher partner prefer-
ence, so reminiscent of the prairie vole males (Lim et al.
2004).

These results, especially the last one which shows that the
normally promiscuous meadow voles can be made to show
greater partner preference, like the prairie voles from whom
they have received a single gene, are undoubtedly of great
significance. Not only do these results unravel the genetic,
physiological and neurological pathway for the causation
of as complex a behaviour as monogamy but they also pro-
vide evidence that a single gene, albeit in the presence of an
appropriate genetic and neural background, can profoundly
affect social behaviour. Quite predictably, the popular press
has gone overboard in reporting these findings. There has
been much discussion about the possibility of using
transgenic technology to make men more monogamous and
more interested in their wives and children! One newspaper
even referred to the behaviour of a past President of the
United States of America. Only time will tell whether these
mechanisms, let alone these technological breakthroughs,
will apply to the human species. But the more significant
import of these results is the credence they lend to the modus
operandi of behavioural ecology which should lead to a more
rapid progress in our understanding of the evolution of other
more complex social behaviours in different animal taxa. In
other words, these results vindicate the behavioural ecolo-
gists’ gambit that assumed the availability of alternative
behavioural phenotypes for the action of natural selection.

The case of the voles is worth dwelling upon a little bit
more. Behavioural ecologists have argued that monogamy
would evolve if the cost of indulging in paternal behaviour
is more than compensated by the benefit in improved off-
spring survival. The difficult question was whether the
mechanisms that produce monogamy and polygamy permit
mutuating from one to the other without creating a lethal
monster. Now we can conclude that this may not be such a
serious problem after all. Indeed, monogamy in the prairie
voles and promiscuousness in the meadow vole appear to
be quite plastic and flexible even within each species. Not
all prairie vole males are equally monogamous: those cap-
tured from a resource-abundant habitat in Illinois fit the
description of monogamy better than those captured from a
more arid habitat in Kansas, in the USA. Crossing the two
Gene transfer makes a vole less promiscuous

populations has shown that hybrid offspring males behaved like their fathers, especially if the father was present up until the birth of the offspring (Roberts et al. 1998). Similarly, not all meadow vole males are equally promiscuous. When forced to cohabit with a single female for periods longer than they would ever do in nature, meadow voles also developed significant preferences for their partners and aggression towards strangers (Parker et al. 2001).

The study of vole mating systems provides the most convincing proof yet of the mutually beneficial impact of simultaneously asking proximate and ultimate questions in behavioural ecology, if ever a proof was needed.

References


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