Crowell[6] presents evidence that glaciation moved across the ancient Gondwana supercontinent following the rotational South Pole deep into the continental interior. Glaciation ended when the South Pole moved offshore. To sustain the argument of Crowley *et al.*, it would have to be assumed that once an ice sheet was initiated it could shift and be maintained as the Pole position shifts into the continental interior. Figure 4 of Crowley *et al.* on page 806, however, shows that with the Pole in the centre of Gondwanaland, summer temperatures are too warm for glaciation. Furthermore, the Pole moved over Antarctica during the Jurassic and Cretaceous[6,7] (213–65 million years ago; see figure), a period noted for its warm, ice-free climate. This evidence also seems to contradict the model of Crowley *et al.* which asserts that glaciation should occur as the pole crosses the continental margin. In my view the record is always unkind to hypotheses that focus on one main cause for the climate record: exceptions can always be found, and these hint that several forcing factors are responsible.

Third, in all fairness, we must question the record of glaciations. The most recent comprehensive compilation suggests that glaciation could have lasted for much of geological time. The timing and extent of glaciation remains a problem. At a recent workshop on the long-term stability of the Earth system at Pennsylvania State University, several speakers suggested that the record of permanent ice is incomplete and that yet further periods could have been glacial. The correlations between cause and effect cannot be accepted too easily — more data are needed. The answers must involve models of ice-sheet growth coupled to models of the complete climate system, and should not depend on inference from the temperature of one season. Data from the geological record already offer many tests of the arguments and will probably yield exceptions to any hypothesis that relies fundamentally on a single causal factor. Crowley *et al.* make an interesting, provocative contribution. Even if we doubt that seasonality is the main factor, we must recognize the importance of the seasonal effect of continental distribution as one of the many factors in climate change. ☐

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Sociobiology

A darwinian theory of divorce

Jared M. Diamond

THE annual divorce rate in monogamous animals can be defined operationally as the percentage of pairs mated in one year, both of whose members survive to the next year and remate with new mates rather than with each other. In well-studied bird species, the divorce rate averages 21 per cent but varies greatly among species (Rowley, I. in *Mate Choice* ed. Bateson, P. 331–360; Cambridge Univ. Press, 1983). At one extreme, the rate is 50–73 per cent in migrant American songbirds which experience 50 per cent annual mortality, so that an individual returning to its previous territory in the spring cannot afford to wait and see whether its previous year's mate also survived to return. At the other extreme, long-lived albatrosses, which spend 1 or 2 years dating and swapping partners before settling on a mate, have rates of only 0–2 per cent. Two recent studies add to accumulating evidence that divorce in some cases is a darwinian adaptation to increase reproductive success.

IMAGE UNAVAILABLE FOR COPYRIGHT REASONS

Colour-banded oystercatcher returning to its eggs. (Courtesy of M. P. Harris).

The first study (Harris, M. P. *et al. Ibis* **129**, 45–57; 1987) involved a British population of oystercatchers whose marital statistics are reminiscent of Hollywood humans. The mating system of these birds is best described as serial monogamy punctuated by widowing or divorce: only one mate in a given year, but up to seven successive mates over the mean breeding life of ten years. No male divorces more than twice, but females divorce up to four times. The annual probability of divorce is highest (18 per cent) after the first year of breeding and decreases to 6 per cent for couples together for 3 years or more. As in humans, there is no clear relation between divorce rate and number of previous marriages, even when the first and fourth marriages of oystercatchers are compared.

It turns out that the best predictor of divorce is reproductive failure in the previous season. The divorce rate is highest for pairs that hatch or fledge no young, and decreases with the number of young produced. Thus, successful fledging of 2 or more young virtually guarantees continued marriage (only 1 divorce in 69 cases), but members of pairs that fledge no young frequently take new mates the next year (43 out of 251). The sole instance of divorce in the middle of the breeding season in this study promptly followed a nesting failure. Although reproductive failure in the first year of mating is disproportionately likely to lead to divorce, a failure in later years of a previously productive marriage has a greater chance of being forgiven. Hence the decision to divorce is based on reproductive history, with the most recent year receiving disproportionate weight.

The second study, of a colony of black petrels in New Zealand, involved smaller sample sizes but yields a similar interpretation (Imber, M. *Notornis* **34**, 19–39; 1987). No pair that succeeded in fledging a chick one season divorced in the next season, whereas one-third of the unsuccessful pairs divorced. As in the oystercatcher study, divorced males retain the pair's territory, and it is the female who moves out to another territory.

What is the adaptive significance of divorce? Reproductive failure can arise from the deficiencies of a mate, from the incompatibility of a pair or from poor cooperation. Hence, a member of an unsuccessful pair might increase its reproductive success by seeking a new mate. At face value, the oystercatcher data suggest that those hoped-for benefits of divorce are elusive, as males hatch or fledge no more young in the immediately post-divorce year than in the pre-divorce year, and a 61 per cent post-divorce improvement in fledging success for females fails to achieve statistical significance. But divorce, whether or not it is eventually beneficial, involves short-term risks, as newly formed pairs of birds tend to fledge fewer young than established pairs. At least for kittiwakes, patience following divorce is rewarded: breeding output declines for at least 2 years post-divorce, but in the long run it pays pairs that fail to hatch eggs to switch mates (Coulson, J. *J. anim. Ecol.* **35**, 269–279; 1966).

Thus divorce, like so many other behaviours, can be explained in darwinian terms. In fact, the criterion of proved reproductive failure that birds use for mate rejection is much more straightforward than the criteria for mate selection, which depends on characters (such as a vigorous song) that may or may not correlate with reproductive success.

Do these studies of birds shed any light on divorce in humans? The parallels at first seem strikingly to suggest that our divorces are ultimately an adaptation to produce and successfully rear more babies. Human divorce is associated with various sorts of marital discord, which would have placed children at risk under the stringent hunter–gatherer conditions prevailing throughout most of human evolution. Middle-aged men tend to desert their grown children and menopausal wife for a younger woman, thereby enabling the scoundrel to father still more children. Men in some societies divorce wives who bear them no children or who bear them only daughters. But such men betray their biological ignorance: the sex of human offspring is determined by sperm rather than egg chromosomes, and male infertility contributes as much as does female infertility to barren marriages. Hence men who divorce for supposed darwinian reasons may only be running away from their own problems. ☐

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Substance K receptor

Return of the magnificent seven

Michael R. Hanley and Trevor Jackson

RECEPTOR cloning is rapidly becoming big business. Historically, it was necessary to implement a daunting programme of purification, structural analysis and rigorous functional assessment to pursue the structure of a particular receptor. But recent innovations in expression cloning may open the door to the systematic cloning of every receptor for which we have a name. On page 836 of this issue[1], Masu *et al.* report the molecular cloning and sequencing of the substance K receptor using only its functional activity in *Xenopus* (toad) oocytes. Its sequencing may present an example of a novel problem for the future: that primary structure (amino-acid sequence) becomes known in the absence of conventional characterization of receptor pharmacology and biochemistry. Moreover, the substance K receptor attracts special interest because it is the first receptor for a neural peptide to be cloned.

Substance K is a member of a family of structurally related peptides called the tachykinins, which share a spectrum of similar biological effects, including actions on sensory processing and inflammation. From several lines of evidence, it now seems likely that each of the three identified mammalian tachykinins may have a corresponding receptor.

The cloning strategy, described in detail by the authors, is conceptually straightforward. They constructed a bovine stomach complementary (c) DNA library in a lambda phage vector containing the SP6 promoter for *in vitro* transcription. The resulting mixture of cDNAs was used to generate a mixture of synthetic messenger (m) RNAs, which was then evaluated for expression of substance K receptor following injection into *Xenopus* oocytes, thus generating an mRNA library. The resulting mixture was taken through a series of fractionations until a single clone was obtained. The appealing aspects of this strategy are that only functionally defined, full-length clones are isolated, and that it should be applicable to any receptor or other gene product that can be assayed by oocyte expression.

It is immediately apparent from the predicted amino-acid sequence that the substance K receptor (SKR) is a single subunit that fits well into the 'seven-transmembrane segment' superfamily of M1- and M2- muscarinic receptors, β_1 and β_2 adrenergic receptors and the rhodopsin-related visual pigments. This designation is based on the prediction, common to each of these sequences, that the receptor is folded so as to cross the membrane seven times. The amino terminus contains two consensus sites for N-linked carbohydrate attachment (Asn residues 11 and 19), placing the first segment on the outside of the membrane. The result of these predictions is to generate a model structure as shown in Fig. 1, with four extracellular and four intracellular segments. The real amino terminus is unknown, but the sequence predicts that the amino terminus may be blocked by covalent fatty acid modification. In other membrane proteins, the Met–Gly sequence is an accurate predictor of amino-terminal conjugation of myristic acid to the Gly residue[2]. This is shown by drawing the first segment as a loop, tethered by the amino terminus. The intracellular segments do not contain any obvious consensus sequences for kinase action, but the authors call attention to a carboxy-terminal segment that is rich in Ser or Thr residues. There are no clearly defined tyrosine kinase sites.

The location of the ligand-binding site in SKR is unknown, but two suggestions have been made for the β_2 adrenergic receptor that may be useful to consider. Based on deletion analysis, the binding site has been suggested[3] to be analogous to the interaction of retinal with opsin, which occurs via transmembrane segment VII. Alternatively, crosslinking studies[1] direct attention to the third extracellular loop and transmembrane segment IV.

It has recently been proposed[5] that peptides and their cognate receptors will show a strict complementarity at the nucleotide level. The cloning of the substance K receptor and the substance K precursor[6] from the same species permits an experimental test of the claimed predictive scheme. The predicted substance K binding site (H-termination–SNKGICFM) is not found in the substance K receptor. Thus, the complementarity hypothesis, reported to be successful in generating antibodies against leutenising-hormone releasing hormone and adrenocorticotropic hormone receptors[6] does not seem applicable to SKR.

The sequence similarity is greatest in the rhodopsin

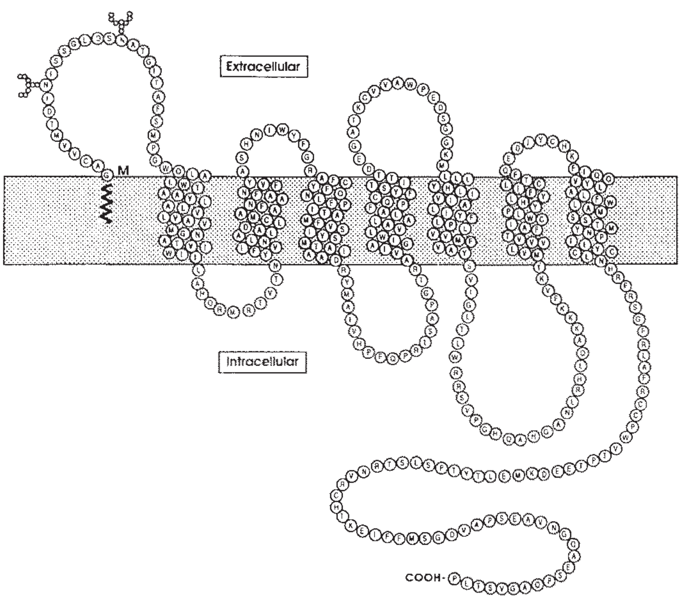

Fig. 1 Possible model for insertion of substance K receptor in the plasma membrane. Membrane-spanning segments are based on predicted hydrophobic transmembrane helices. The standard one-letter code for amino-acid residues is used. Also noted are the potential sites of N-linked glycosylation and myristylation at the predicted amino-terminal glycine.