cannot dampen cell proliferation, but neither can it influence migration.

Another confounding factor is that Rho proteins control a wide range of signalling pathways, which, when deregulated, can result in various cellular abnormalities[13]. As well as influencing migration, these proteins might affect cell survival, growth and differentiation[6], thereby influencing tumour development and progression[7]. You won't be surprised to hear, then, that it will be a challenge to determine whether p27[Kip1] contributes to tumour progression *in vivo* via regulation of the cell cycle, or Rho-mediated signalling, or both. The answer awaits the generation of mice in which wild-type p27[Kip1] is replaced by a mutant version that lacks the binding domain for either cyclin–CDK complexes or RhoA. All being

well, these studies will reveal the true role of p27[Kip1] in cancer.

John G. Collard is at the Netherlands Cancer Institute, Division of Cell Biology, Plesmanlaan 121, 1066 CX Amsterdam, The Netherlands.
e-mail: j.collard@nki.nl

1. Besson, A., Gurian-West, M., Schmidt, A., Hall, A. & Roberts, J. M. *Genes Dev.* **18**, 862–876 (2004).
2. Philipp-Staheli, J., Payne, S. R. & Kemp, C. J. *Exp. Cell Res.* **264**, 148–168 (2001).
3. Philipp-Staheli, J. *et al. Cancer Cell* **1**, 355–368 (2002).
4. Slingerland, J. & Pagano, M. *J. Cell. Physiol.* **183**, 10–17 (2000).
5. McAllister, S. S., Becker-Hapak, M., Pintucci, G., Pagano, M. & Dowdy, S. F. *Mol. Cell. Biol.* **23**, 216–228 (2003).
6. Ridley, A. J. *et al. Science* **302**, 1704–1709 (2003).
7. Malliri, A. & Collard, J. G. *Curr. Opin. Cell Biol.* **15**, 583–589 (2003).
8. Friedl, P. & Wolf, K. *Nature Rev. Cancer* **3**, 362–374 (2003).
9. Sahai, E. & Marshall, C. J. *Nature Cell Biol.* **5**, 711–719 (2003).
10. Goukassian, D. *et al. FASEB J.* **15**, 1877–1885 (2001).
11. Kouvaraki, M. *et al. Cancer* **94**, 2454–2465 (2002).
12. Saez, A. *et al. Br. J. Cancer* **80**, 1427–1434 (1999).
13. Boettner, B. & van Aelst, L. *Gene* **286**, 155–174 (2002).

Animal behaviour

Fickle females?

Michael J. Ryan

The courtship of satin bowerbirds is a complicated business. Different parts of a male's display appeal to females of different ages, so age-biased variation might underlie the evolution of these displays.

A common complaint among courting men is that women do not know what they want. Virgil, for instance, observed that "A woman is always a fickle, unstable thing". How, then, can a male cope? One solution would be to assess the general preference in this sea of shifting female wants and desires, and bias courtship to the majority opinion. Another would be to appeal simultaneously to multiple preferences, to be something to everyone. This second solution, we are told by Coleman and colleagues on page 742 of this issue[1], is the one adopted by male satin bowerbirds (*Ptilonorhynchus violaceus*).

These males have a complex set of courtship rituals. They decorate their bowers with blue objects, and they also combine a suite of vocalizations and movements into a behavioural display directed at females. Another layer of complexity derives from the timing of these display components. In the first stage of courtship a male is not present at the bower but his decorations are. Thus, the only way for a female to evaluate the male is through this evidence. In the second stage, a female returns to a subset of the original bowers she sampled. During this stage, both bower decorations and the male, who intensely courts the female, are present (Fig. 1), and the female builds nests at several bowers. In the final stage, the female makes several visits to where she constructed nests and decides on a single mate.

Coleman and colleagues' experiments[1] were underpinned by an observation from

a study[2] by members of the same group. Younger females, it turned out, are more threatened by the physical male displays than are older females. Could variation in this female fear factor generate selection for complex displays in males? In experiments conducted over a two-year period, Coleman *et al.* addressed the question by augmenting some bowers with extra decorations (treatment bowers) while leaving others unmanipulated (control bowers). Using video recordings, they determined the effect of bower treatment on the frequency of visits by females of different ages — first year, second year and three-plus years — at each of the three stages of courtship.

Of the bowers sampled during the first stage of courtship, all females were more likely to return to treated rather than control bowers in the second stage (remember, males are not present during the first stage). The same was not true, however, when females moved from the second stage, when the male is present and subjects the females to intense displays, to the third stage. Whereas younger females were more likely to visit the experimental than control bowers in the third stage, augmented bower decorations had no such effect on the behaviour of older females.

During the final stage of courtship, females decide on a mate. Here again there is an age-biased effect of bower treatment. In both years of Coleman and colleagues' study, first-year females preferred to mate with males in more decorated bowers, but the treatment did not influence the mate choice

of the three-plus-year females. In year 1 of the study, the second-year females' choice of mate showed no effect of bower treatment, but they did in year 2, when even more decorations were added.

An age-biased effect is not restricted to female responses to bower decorations, but also applies to male display intensity. The more intense the male display during the second stage of courtship, the more likely were older females to visit a male in the third stage. But that did not apply to the two younger cohorts. Coleman *et al.*[1] conclude that selection generated by age-biased variation in female choice is responsible for the evolution of complex courtship in these bowerbirds. The fear that the male's display instils in younger females seems to drive the age-biased differences in courtship preference.

Clearly, the further elaboration of bower decorations to the degree used in the manipulations would be under stronger selection from younger rather than older females. In this study, however, it is not clear if older females would generate selection to maintain the current level of bower decorations. Perhaps there is a lower threshold for this component of the display in older than in younger females; if so, older females alone could generate the selection needed to maintain this complex display. The fact that second-year females were not influenced by augmented bower decorations in year 1 of the study, but were in year 2 when more decorations were used, suggests that thresholds for an effect might change continuously with age. This age class could also offer a target group for research to understand the relative value of decorations and male display intensity for females of different ages.

A larger question concerns the evolutionary pattern of bowerbird displays. The complexity of bowers, decorations and courtship behaviour varies greatly among different species of bowerbird[3,4]. Can these broad macroevolutionary patterns among species be explained by the same microevolutionary process suggested by the findings of Coleman *et al.*[1]?

Studies of fish[5], frogs[6], cockroaches[7] and humans[8] have shown that female mating preferences can change as a function of female age, size and reproductive status. Such variation in preferences can contribute to the maintenance of variation in male traits. Young female guppies, for example, prefer males with more orange pigmentation, whereas older females are agnostic about colour and seem to prefer courtship vigour[5]; larger female cricket frogs prefer lower-frequency mating calls, but smaller females prefer higher-frequency calls[6]. What is unusual in the case of satin bowerbirds is that the variation in female mating preferences more clearly contributes to the evolution of multi-component and

Figure 1 **Performance art — a male bowerbird displays as a female assesses the show from the bower.**

multi-modal male displays. There is much interest in the functional significance of complex displays[9], especially those that involve different senses. We see here that one explanation is that different components of such signals might be aimed at different audiences. We also see, at least in bowerbirds, that females aren't fickle: they just change their mind.   ∎

Michael J. Ryan is in the Section of Integrative Biology, University of Texas, Austin, Texas 78712, USA.
e-mail: mryan@mail.utexas.edu

1. Coleman, S. W., Patricelli, G. L. & Borgia, G. *Nature* **428**, 742–745 (2004).
2. Patricelli, G. L., Uy, J. A. & Borgia, G. *Behav. Ecol.* (in the press).
3. Gilliard, T. E. *Birds of Paradise and Bower Birds* (Weidenfeld & Nicholson, London, 1969).
4. Borgia, G. *Sci. Am.* **254** (June), 92–100 (1986).
5. Kodric-Brown, A. & Nicoletto, P. *Am. Nat.* **157**, 316–323 (2001).
6. Ryan, M. J., Perrill, S. A. & Wilczynski, W. *Am. Nat.* **139**, 1370–1383 (1992).
7. Moore, P. J. & Moore, A. J. *Proc. Natl Acad. Sci. USA* **98**, 9171–9176 (2001).
8. Wedekind, C., Seebeck, T., Bettens, F. & Paepke, A. *Proc. R. Soc. Lond. B* **260**, 245–249 (1995).
9. Partan, S. & Marler, P. *Science* **283**, 1272–1273 (1999).

Meteorology

Testing time for El Niño

David Anderson

Analyses that largely exploit indirect data from the past 150 years show that El Niño and La Niña might be more predictable than was thought. The results presage the prospect of extended climate forecasts.

Some of the worst famines in history were those of around 1877, a period in which perhaps 40 million people died in India and China[1]. This and later disasters inspired meteorologists to try to predict whether the monsoon rains would be plentiful or sparse. The paper by Chen *et al.* on page 733 of this issue[2] is in this tradition. The authors have tested a model of the behaviour of the ocean and atmosphere to 'predict' the occurrence of ENSO (El Niño/Southern Oscillation), a phenomenon rooted in the equatorial Pacific Ocean but which has widespread climatic consequences.

From the early monsoon research, an appreciation emerged of the Southern Oscillation and some of its near-global impacts; later on, the connection to the periodic warming in the central–east equatorial Pacific Ocean known as El Niño was clarified. The science of seasonal forecasting and El Niño prediction was born as a result of the famines of the late 1800s, although it was a century before forecasts based on models of the ocean and atmosphere were developed. The term ENSO encompasses the cold as well as the warm state of the equatorial Pacific — that is, it includes La Niña as well as El Niño.

A major requirement for seasonal forecasting is an ability to predict ENSO events, which continue to have the potential to cause widespread disruption. For example, 1997–99 saw one of the largest El Niños in the instrumental record (Fig. 1, overleaf), followed by La Niña. Damage was estimated to exceed US$20 billion, although beneficial effects in certain regions possibly offset this figure. If ENSO events can be predicted, steps can be taken to mitigate the losses. So successful forecasting of ENSO variability would be of great practical benefit. But such forecasting is immensely challenging, one difficulty being that the number of past events on which models can be tested is quite small owing to the lack of data. Chen *et al.*[2], however, have been able to test their model on events stretching back to before the 1877 El Niño, thus covering a much longer period than is normally considered.

From their results, the authors argue that a large ENSO event might be predictable two years in advance, much longer than hitherto expected. For example, their Fig. 3 (page 734) shows forecasts of six of the largest El Niños since 1856, including that of 1997–98. Even forecasts begun two years before the peak of the latter at the end of 1997 are reasonably good; and those from October 1996 capture the growth, maturity and decay in 1998 very well. These results are all the more impressive given that an earlier version of this model failed totally during the 'real-time' forecasting of the 1997–98 event. Many other models also performed poorly for this period[3], although there was some success at the shorter range of a few months[4].

So why are the new forecasts so much better than before? A major source of difficulty in climate prediction is model error, possibly the single biggest problem with physically based models. One way to deal with the issue is to improve the models, but this is a long, hard process; another is to accept that a model has error, but to try to mitigate the effects. That is what Chen *et al.* have done. To allow for model errors, corrections are made to the ocean state and to the sea surface temperature (SST) before its effects are 'passed' to the atmosphere; and corrections are made to the atmospheric wind before it is used to drive the ocean. ENSO forecasting requires knowledge of the ocean initial conditions and, to a small extent, those of the atmosphere. Through their strategy for correcting model error, Chen *et al.* also produce better initial conditions.

The 'training period' for deriving the model corrections is 1980–2000. As this includes both the 1997–98 event and the other big El Niño of 1982–83, there could be some artificial 'skill' in the predictions of this event. In general, the more choices and tunable parameters in a forecast methodology, the greater the risk of overestimating the forecast skill. Nonetheless, as the number of