sexual selection may be reversed: from the traditional strategy of producing many tiny sperm, fostering anisogamy, to the production of ever larger, ever fewer sperm, a counterintuitive runaway from anisogamy.

The new work of Bjork and Pitnick [16] indicates that, when sperm size plays an important role in sperm competition, the evolutionary trajectory of sperm traits under sexual selection is more difficult to predict. This may shed new light on recent studies showing that sperm competition may sometimes favour the production of longer [17–19] or larger [20] sperm, not necessarily of more sperm.

References

1. Parker, G.A., Baker, R.R., and Smith, V.G.F. (1972). The origin of evolution of gamete dimorphism and the male-female phenomenon. J. Theor. Biol. *36*, 529–553.
2. Trivers, R.L. (1972). Parental investment and sexual selection. In Sexual selection and the descent of man, B. Campbell, ed. (Chicago: Aldine Publishing Company), pp. 52–97.
3. Clutton-Brock, T.H., and Parker, G.A. (1992). Potential reproductive rates and the operation of sexual selection. Quart. Rev. Biol. *67*, 437–456.
4. Shuster, S.M., and Wade, M.J. (2003). Mating systems and strategies (Princeton: Princeton University Press).
5. Bateman, A.J. (1948). Intrasexual selection in Drosophila. Heredity *2*, 349–368.
6. Parker, G.A. (1970). Sperm competition and its evolutionary consequences in insects. Biol. Rev. *45*, 525–567.
7. Birkhead, T.R., and Pizzari, T. (2002). Postcopulatory sexual selection. Nat. Rev. Genet. *3*, 262–273.
8. Dziuk, P.J. (1996). Factors that influence the proportion of offspring sired by a male following hererospermic insemination. Anim. Repro. Sci. *43*, 65–88.
9. Martin, P.A., Reimers, T.J., Lodge, J.R., and Dziuk, P.J. (1974). The effect of ratios and numbers of spermatozoa mixed from two males on proportions of offspring. J. Reprod. Fertil. *39*, 251–258.
10. Parker, G.A. (1982). Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. J. Theor. Biol. *96*, 281–294.
11. Pitnick, S. (1996). Investment in testes and the cost of making long sperm in *Drosophila*. Am. Nat. *148*, 57–80.
12. Harcourt, A.H., Harvey, P.H., Larson, S.G., and Short, R.V. (1981). Testis weight, body weight and breeding system in primates. Nature *293*, 55–57.
13. Ramm, S.A., Parker, G.A., and Stockley, P. (2005). Sperm competition and the evolution of male reproductive anatomy in rodents. Proc. R. Soc. Lond. B. *272*, 949–955.
14. Hosken, D.J., and Ward, P.I. (2001). Experimental evidence for testis size evolution via sperm competition. Ecol. Lett. *4*, 10–13.
15. Pitnick, S., Spicer, G.S., and Markow, T.A. (1995). How long is a giant sperm? Nature *375*, 109.
16. Bjork, A., and Pitnick, S. (2006). Intensity of sexual selection along the road to isogamy. Nature, in press.
17. Miller, G.T., and Pitnick, S. (2002). Sperm-female coevolution in *Drosophila*. Science *298*, 1230–1233.
18. Gage, M.J.G. (1994). Associations between body size, mating pattern, testis size, sperm lengths across butterflies. Proc. R. Soc. Lond. B. *258*, 247–254.
19. LaMunyon, C.W., and Ward, S. (2002). Evolution of larger sperm in response to experimentally increased sperm competition in *C. elegans*. Proc. R. Soc. Lond. B. *269*, 1125–1128.
20. Oppliger, A., Naciri-Graven, Y., Ribi, G., and Hosken, D.J. (2003). Sperm length influences fertilization success during sperm competition in the snail *Viviparus ater*. Mol. Ecol. *12*, 485–492.

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Animal Cognition: Monkey Meteorology

Mangabey monkeys have been shown to rely on memory of recent trends in temperature and solar radiation to decide whether to feed on a particular patch of fruit. These observations reveal a rich mental representation of the physical environment in monkeys and suggest foraging may have been an important selective pressure in primate cognitive evolution.

Michael Platt

People love to talk about the weather, and not just because it provides an easy entrée into conversation. Weather forecasts help us to plan our days, elect to wear a heavy coat or take along an umbrella, decide when to plant our crops, or scrub a planned spacecraft launch. Their utility is evident in the earliest written documentation of weather patterns by the ancient Greeks and Chinese over 2000 years ago (for example, Aristotle's *Meterologica*). Incised bone fragments from the Paleolithic may track the lunar cycle, raising the possibility that even pre-historic humans kept astronomical records useful in forecasting the weather [1]. Even today, the Weather Channel remains an exceptionally popular media outlet, reaching over 89 million households in the U.S. and consistently ranked in the top 15 of all web sites, despite inevitable inaccuracies in forecasting even with modern meterological methods.

But is this fascination with the weather uniquely human? After all, weather information would appear to be equally useful for animals, for example in planning group movements [2] or timing reproduction [3]. A particularly compelling problem confronting many animal species is choosing where to forage for food. It seems reasonable to suppose that foraging decisions could be improved by taking weather into account, as the quantity and quality of many foods is strongly influenced by recent meteorological trends [4]. In savannah habitats, for example, rainfall patterns largely determine the availability of ripe fruits [4], whereas consistently warm seasonal temperatures lower the nutritional quality of grasses [5].

Despite the obvious utility of meteorological information for guiding foraging decisions, conclusive evidence for its use by animals remains elusive. Prior studies have demonstrated that current weather conditions influence behavior, for example when animals seek shade during the midday heat or huddle together when cold, and that activity patterns in general can be indirectly influenced by the affects of weather on food availability [4]. In this issue of *Current Biology*, Janmaat *et al.* [6] provide compelling new evidence that monkeys actually make decisions about where to forage based, at least in part, on stored information about recent trends in weather. These observations imply that monkeys possess sophisticated knowledge of the aggregate effects of temperature and solar radiation on food quality, and use this information to enhance their own foraging efficiency.

These conclusions are based on detailed observations of the feeding and ranging behavior of grey-cheeked mangabeys (*Lophocebus albigena*), medium-sized monkeys inhabiting tropical forests in western Africa. The authors followed a group of 18–24 of these primates from dawn until dusk for 210 days over the course of a single year. Prior to the observation period, Janmaat *et al.* [6] mapped out the locations of 80 fig trees, the principal source of fruit in the monkeys' diet, within the roughly 600 hectare home range of the animals. Each day, the authors noted the quantity and quality of fruit, as well as the presence and maturation of weevil larvae (a tasty and nutritional treat) within the figs, in any of these trees when the monkey group approached within 100 metres, and recorded the position of the group every 10 minutes using a satellite global positioning system (GPS).

As figs tend to ripen more quickly during warm, sunny weather, and weevil larval development also depends on temperature, Janmaat *et al.* [6] predicted that mangabeys ought to be more likely to revisit a fig tree following a period of warm and sunny days compared with cool and cloudy days. In fact, they found that the probability that the monkeys would revisit any particular fig tree was a linear function of the average maximum ambient temperature over the prior week [6]. The probability of revisiting a fig tree was also higher following days with high solar radiation, as measured with a light meter. Together, these data suggest that monkeys use recent weather trends to inform their foraging decisions.

One alternative to this hypothesis is that mangabeys are able to use sensory cues emanating from the fruits themselves. That is, perhaps fruits became brighter, more colorful, or more aromatic following warm and sunny days, and monkeys used these cues to decide whether or not to approach a given tree. To address this issue, Janmaat *et al.* [6] performed an analysis of data for trees devoid of any ripe fruit when the monkeys revisited them. Such trees could still be potentially valuable to the monkeys since even unripe fruits are often infested with weevil larvae, which cannot be detected at a distance. The authors found that monkeys were also more likely to revisit these trees following a period of warm and sunny weather, thus ruling out the simple use of sensory cues. They also demonstrated that foraging decisions did not appear to be based on a simple learned association, or rule, linking the experience of finding ripe fruit in a tree with the experience of warmth, as the ambient temperature on the first visit did not predict whether monkeys would return to the tree. Moreover, monkeys were no more likely to return to a fig tree on a particularly warm day, nor were the generally more active and thus more likely to come across trees with ripe figs on particularly warm days.

Together, these data suggest monkeys somehow represent the time integral of temperature and solar radiation over the previous week or so, and use this information to guide foraging decisions. Moreover, these data also indicate that monkeys remembered the location and content of previously visited fig trees, and then chose whether or not to exploit them based on stored information about recent trends in weather. Exactly how the monkeys assessed and stored this information remains unknown. Once acquired, however, the time integral of temperature could directly modulate the strength of the internal discount function relating estimated reward value to the delay between fruit tree visits [7]. Neurobiological studies suggest that representations of goals in the primate brain are scaled by their discounted reward value [8,9], and thereby bias subsequent choices to more valuable options. Such a model of reward discount functions scaled by recent trends in temperature could provide a simple mechanistic account of the influence of weather on mangabey foraging decisions, but remains to be tested experimentally.

The present study [6] complements recent work demonstrating that many animals use remembered information about the environment to make decisions. In particular, learned information about the location and quality of food sources appears to play an important role in determining foraging patterns in primates [10–12]. It has been argued that the relatively large brains and enhanced cognitive capacity of primates may have evolved, in part, to solve the complex problems presented by a diet high in fruit, which ripens intermittently in often widely separated locations [13,14], and thus the ability to transduce and store information about recent trends in temperature and solar radiation may be viewed as an essential mental ability shaped by natural selection to enhance foraging efficiency. Testing this idea would require probing the influence of weather patterns on foraging decisions made by other primates that specialize on other types of foods, such as leaves or insects, which are not thought to require much cognitive capacity to acquire (compare [15]). Nonetheless, Janmaat *et al.* [6] provide compelling new evidence for meteorology in monkeys.

References

1. Marshack, A. (1991). The Tai plaque and calendrical notation in the Upper Paleolithic. Camb. Archaeol. J. *1*, 25–61.
2. Bronikowski, A.M., and Altmann, J. (1996). Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. Behav. Ecol. Sociobiol. *39*, 11–25.
3. Lee, P.C. (1987). Nutrition, fertility, and maternal investment in primates. J. Zool. *213*, 409–422.
4. Richard, A.F. (1985). Primates in Nature, (New York, New York: W.H. Freeman and Company).
5. Dunbar, R.I.M., Hannah-Stewart, L., and Dunbar, P. (2002). Forage quality and the costs of lactation for female gelada baboons. Anim. Behav. *64*, 801–805.
6. Janmaat, K.R.L., Byrne, R.W., and Zuberbuhler, K. (2006). Primates take weather into account when searching for fruits. Curr. Biol. *16*, 1232–1237.
7. Mazur, J.E. (1987). An adjusting procedure for studying delayed

reinforcement. In Quantitative Analysis of Behavior: Vol. 5. The Effect of Delay and of Intervening Events on Reinforcement Value, M.L. Commons, J.E. Mazur, J.A. Nevin, and H. Rachlin, eds. (Hillsdale, New Jersey: Erlbaum), pp. 55–83.
8. Sugrue, L.P., Corrado, G.S., and Newsome, W.T. (2004). Matching behavior and the representation of value in the parietal cortex. Science *304*, 1782–1787.
9. Roesch, M.R., and Olson, C.R. (2005). Neuronal activity in primate orbitofrontal cortex reflects the value of time. J. Neurophysiol. *94*, 2457–2471.
10. Garber, P.A. (1989). Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. Am. J. Primatol. *19*, 203–216.
11. Menzel, C.R. (1991). Cognitive aspects of foraging in Japanese monkeys. Anim. Behav. *41*, 397–402.
12. Janson, C.H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Anim. Behav. *55*, 1129–1143.
13. Clutton-Brock, T.H., and Harvey, P.H. (1980). Primates, brains and ecology. J. Zool. Soc. Lond. *190*, 309–323.
14. Milton, K. (1979). Spatial and temporal patterns of plant food in tropical forests as a stimulus to intellectual development in primates. Am. J. Phys. Anthropol. *50*, 464–465.
15. Platt, M.L., Brannon, E.M., Briese, T.L., and French, J.A. (1996). Differences in feeding ecology predict differences in performance between golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*) on spatial and visual memory tasks. Anim. Learn. Behav. *24*, 384–393.

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Cell Biology: Ran, Mitosis and the Cancer Connection

The small GTPase Ran has been shown to regulate HURP, a protein that interacts with several mitotic spindle assembly factors. This discovery sheds new light on the role of Ran in the fidelity of mitosis and in cancer.

Helen S. Sanderson and Paul R. Clarke

Cell division requires that one copy of each chromosome is faithfully segregated to each of the daughter cells during mitosis, a remarkable feat that is achieved by the mitotic spindle, a bipolar array of microtubules focussed at each pole by a centrosome. One of the most important features of a successful mitosis is the proper biorientation of all chromosomes on the spindle. This is accomplished through the attachment of microtubules to the kinetochore region of each chromosome, and the stabilization and bundling of microtubules to form kinetochore fibres (k-fibres). Biorientation and congression of a chromosome to the middle of the spindle is relatively slow, but once achieved, may serve as a highway for monoorientated chromosomes, that is those attached to microtubules from only one pole of the spindle, enabling them to hitchhike to the centre of the cell where the density of searching spindle microtubules is high [1,2]. Until all chromosomes are successfully attached to microtubules in a biorientated manner, with each kinetochore from the duplicated sister chromatids attached to microtubules from opposite poles of the spindle, the spindle checkpoint prevents separation of the chromatids and premature cell division. When the fidelity of this process is compromised, abnormal numbers of chromosomes can be distributed to the daughter cells (aneuploidy), which is often associated with cancer.

Embedded at the regulatory heart of these processes is the small GTPase Ran. The active GTP-bound configuration of Ran is generated by the chromatin-associated guanine nucleotide exchange factor RCC1 and promotes the release of spindle assembly factors from inhibitory complexes with importins [3]. The generation of Ran-GTP at chromosomes is proposed to guide spindle assembly by providing a positional gradient signal, which has been visualised using fluorescent reporters in *Xenopus* egg extracts and mammalian cells, most recently by Caudron *et al.* [4] and Kalab *et al.* [5]. Of the growing portfolio of factors which fall under the aegis of mitotic regulation by Ran-GTP and importins, perhaps the most prominent identified to date is TPX2, which when released from importin-α triggers activation of the Aurora A protein kinase [6]. During mitosis, activated Aurora A phosphorylates a broad array of proteins, including the tumour suppressors Lats2 and BRCA1, and the close association of Aurora A with the development of human cancers tallies with its central role in centrosome functioning and mitotic progression [7].

Two papers published recently in *Current Biology* [8,9] show that another oncoprotein, hepatocarcinoma-upregulated protein (HURP), is under the direct regulatory control of Ran during mitosis (Figure 1). HURP was first identified as a potential oncogene that is aberrantly expressed in human hepatocellular carcinoma [10]. The expression profile of HURP correlates with that of Aurora A, being periodically expressed during the cell cycle and peaking at G2/M. HURP is a substrate for the kinase, suggesting that they may be coordinately regulated through stabilisation of HURP by Aurora A [11]. In the new studies, Koffa *et al.* [8] employed *Xenopus* extracts to identify novel mitotic targets of Ran that promote bipolar spindle formation and characterised a HURP-containing complex with such activity. They demonstrated that HURP is a microtubule-associated protein (MAP) in mitotic extracts [8]. Complementary cell analyses by Silljé *et al.* [9] revealed a striking subcellular distribution, with HURP residing predominantly at k-fibres in prometaphase, where it remains until telophase when cellular levels sharply decline. This