

Several of the mechanisms of gastrulation are conserved among vertebrates [18]. However, the newly described early convergence extension mechanism of the epiblast that takes place at the very beginning of gastrulation appears to be specific to amniotes. This phase might explain the evolutionary change of shape of the blastopore, from a circular structure to the radial slit shape characteristic of the primitive streak.

References

1. Gräper, L. (1929). Die Primitiventwicklung des Hühnchens nach stereokinematographischen Untersuchungen, kontrolliert durch vitale Farbmarmierung und verglichen mit der Entwicklung anderer Wierbeltiere. *Arch. EntwMech. Org.* 116, 382–429.
2. Wetzel, R. (1929). Untersuchungen am Hühnchen. Die Entwicklung des Keims während der ersten beiden Bruttage. *Arch. EntwMech. Org.* 119, 188–321.
3. Cui, C., Yang, X., Chuai, M., Glazier, J.A., and Weijer, C.J. (2005). Analysis of tissue flow patterns during primitive streak formation in the chick embryo. *Dev. Biol.* 284, 37–47.
4. Chuai, M., Zeng, W., Yang, X., Boychenko, V., Glazier, J.A., and Weijer, C.J. (2006). Cell movement during chick primitive streak formation. *Dev. Biol.* 296, 137–149.
5. Vakaet, L. (1970). Cinephotomicrographic investigations of gastrulation in the chick blastoderm. *Arch. Biol.* 87, 387–426.
6. Wei, Y., and Mikawa, T. (2000). Formation of the avian primitive streak from spatially restricted blastoderm: evidence for polarized cell division in the elongating streak. *Development* 127, 87–96.
7. Chuai, M., and Weijer, C.J. (2007). 4 the mechanisms underlying primitive streak formation in the chick embryo. *Curr. Top. Dev. Biol.* 87, 135–156.
8. Newman, T.J. (2007). 5 grid-free models of multicellular systems, with an application to large-scale vortices accompanying primitive streak formation. *Curr. Top. Dev. Biol.* 87, 157–182.
9. Lawson, A., and Schoenwolf, G.C. (2001). Cell populations and morphogenetic movements underlying formation of the avian primitive streak and organizer. *Genesis* 29, 188–195.
10. Keller, R., Davidson, L.A., and Shook, D.R. (2003). How we are shaped: the biomechanics of gastrulation. *Differentiation* 71, 171–205.
11. Voiculescu, O., Bertocchini, F., Wolpert, L., Keller, R.E., and Stern, C.D. (2007). The amniote primitive streak is defined by epithelial cell intercalation before gastrulation. *Nature* 449, 1049–1052.
12. Shih, J., and Keller, R. (1992). Cell motility driving mediolateral intercalation in explants of *Xenopus laevis*. *Development* 116, 901–914.
13. Bertet, C., Sulak, L., and Lecuit, T. (2004). Myosin-dependent junction remodelling controls planar cell intercalation and axis elongation. *Nature* 429, 667–671.
14. Seifert, J.R., and Mlodzik, M. (2007). Frizzled/PCP signalling: a conserved mechanism regulating cell polarity and directed motility. *Nat. Rev. Genet.* 8, 126–138.
15. Wallingford, J.B., Rowning, B.A., Vogeli, K.M., Rothbacher, U., Fraser, S.E., and Harland, R.M. (2000). Dishevelled controls cell polarity during *Xenopus* gastrulation. *Nature* 405, 81–85.
16. Bertocchini, F., and Stern, C.D. (2002). The hypoblast of the chick embryo positions the primitive streak by antagonizing nodal signaling. *Dev. Cell* 3, 735–744.
17. Waddington, C.H. (1932). Experiments on the development of chick and duck embryos cultivated in vitro. *Phil. Trans. R. Soc. Lond. B* 221, 179–230.
18. Solnica-Krezel, L. (2005). Conserved patterns of cell movements during vertebrate gastrulation. *Curr. Biol.* 15, R213–R228.

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Sexual Conflict: The Battle of the Sexes Reversed

In most species one sex is more reluctant to mate than the other. Standard explanations invoking potential reproductive rates have shortcomings that are illustrated by a new study of eager female and reluctant male antelopes.

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Females reject mating opportunities more often than males. Theoretical explanations for this widespread pattern usually highlight a sex difference in potential reproductive rate. This refers to the maximum rate at which parents can produce independent offspring if access to mating partners is unconstrained [1]. It is usually higher for males because sperm are smaller than eggs, so they can be produced rapidly in large quantities. Also, given the disparity in gamete size, the total investment in all gametes that are expended per mating is often smaller for males than for females. Males, therefore, have to accumulate fewer resources before they can mate again. Finally, with the notable exception of fishes and frogs, the females of most species tend to provide more prolonged parental care than males [2], and this extended

parental investment delays their return to the pool of potential mates. The net effect of these factors is that males generally have a higher potential reproductive rate than females [1].

A higher potential reproductive rate means that males can re-enter the mating pool sooner than females. Consequently, the sex ratio of individuals that are capable of mating, the operational sex ratio, becomes male-biased [3]. Males end up competing for a limited number of females, while females encounter an excess of potential mates. Sometimes it can be beneficial for females to wait for a better partner because this can increase breeding success or improve offspring quality [4]. Waiting for the right partner has its own costs though, and females are more likely than males to benefit by rejecting current mates because a male-biased operational sex ratio reduces the likely wait.

Despite the intuitive appeal of reasoning based on the potential

reproductive rates of males and females there are hidden pitfalls. For a start, we need to consider how other factors, such as the adult sex ratio, affect the operational sex ratio. Cardinalfish males are mouth-brooders that protect fertilized eggs within their mouths until they hatch. Thus, cardinalfish males have a lower potential reproductive rate than females; however, females have a higher mortality rate, so there is still a surplus of males willing to provide paternal care and females do not compete for males [5]. More generally, the potential-reproductive-rate approach relies on the unsatisfactory abstraction of potential rates even though selection acts on actual rates of reproduction. Potential reproductive rates can be extremely misleading when trying to explain why females more often provide parental care. A still widespread argument is that caring males forego more mating opportunities than caring females, but this rests on the false premise that males do actually reproduce at a higher rate than females. Unless the adult sex ratio is biased, this is impossible because each offspring has one mother and one father [4,6]. Another challenging aspect of calculating potential reproductive rate is deciding what constitutes ‘unconstrained



Figure 1. Topi antelope triad.

A triad consisting of a territorial topi male (right) and two visiting females on a lek in Masai Mara National Reserve, Kenya. Photograph: Jakob Bro-Jørgensen.

access to mates'. This is especially problematic when females are promiscuous so that male reproductive success with a given female depends on his ejaculate size and the number of ejaculates he transfers compared to his rivals. What does unconstrained access mean in this context?

Despite these problems, many biologists might subscribe to the view that potential reproductive rate only fails to explain sex roles under unusual circumstances. In most species, the potential reproductive rate differs so markedly between males and females that minor modifications to theory seem unlikely to alter the bigger picture. However, a recent study on Kenyan topi antelopes (Figure 1) published in *Current Biology* by Bro-Jørgensen challenges this view [7]. Breeding male topi form a tight aggregation for the exclusive purpose of attracting mates (a 'lek'). Males spend considerable effort competing for a central position on the lek. Females visit the lek, mate and then leave. As females are the sole care-providers, they have a much lower potential reproductive rate than males. Given the effort males expend on acquiring a territory, and the proximity of competitors, a lek seems to be the last place where a male should reject mating opportunities. But this is exactly what occurs.

Bro-Jørgensen [7] noted occasions when a male simultaneously encountered two females who wanted to mate with him ('triads'). Despite preferring certain males, at least 73% of females mate multiple times, and the resulting sperm competition favours larger ejaculates [8]. Females also mate repeatedly with the same male during their one-day oestrus, so preferred males can have more than 45 matings per hour. Although direct evidence from topi is lacking, studies on other large ungulates suggest that under these circumstances males will become sperm depleted [9]. Males must, therefore, decide how often to mate with each female. Each successive mating with a female increases a male's likely share of paternity by a diminishing amount, so a male should favour the female that he has mated with fewer times. Indeed, Bro-Jørgensen [7] showed that males in triads were more likely to switch partners after they have mated several times with the same female. However, a female that aggressively attacked the mating pair increased her chance of being the next to mate.

This indicates that in topi antelopes sexual conflict over mating rates occurs in the opposite direction to that predicted by potential reproductive rates. Females were more eager to mate than males and competed with each other for matings. In contrast,

males rejected mating opportunities by counterattacking a female if they had mated with her disproportionately often. Of course, the constellation of factors that make the use of potential reproductive rate misleading in topi might be seen as aberrant, but an almost identical phenomenon occurs in a lekking bird, the great snipe [10]. Moreover, decreased male interest in mating with a prior mate is so well known that it has had its own moniker — the Coolidge effect — for 45 years [11].

We can draw at least two lessons from Bro-Jørgensen's study [7]. First, it can be misleading to focus on absolute investment prior to and after a mating and the consequent potential reproductive rate of each sex. The material cost of male investment — a short bout of pelvic thrusting and a modest ejaculate — are minuscule when compared to those of a female — preparing the uterus, gestation and lactation. We should remind ourselves that mating not only involves sexual conflict over access to mates but also conflict among the various options available to an individual. A sperm-depleted male might lose an opportunity to sire offspring with a new female, especially if she has mated multiply. Such opportunity costs become prohibitive if males can sometimes mate in quick sequence with several females. This, of course, begs a question: why don't males have larger testes? A plausible answer is that the peak mating rate of a popular male is so high, and its occurrence so infrequent, that sexual restraint is a more economical response than capital investment in the machinery needed to ejaculate continually at peak capacity.

Second, reassessment of theory — no matter how widely accepted — is always worthwhile. Evolutionary theorists are fussy about constructing logical arguments and identifying directions of causality. Such debates can appear arcane, unless they change predictions about what we will observe in nature. Does it really matter whether sexual selection drives differences in parental investment or vice versa [12–15]? The case of the reluctant male topi shows that it does: Accurate predictions depend on getting the logical steps right. The potential reproductive rate is a strong, albeit imperfect, determinant of the operational sex ratio [3], but using the

operational sex ratio as a shortcut to identify the direction of sexual competition and mate choice might be too much of a simplification [16]. Using only the operational sex ratio implicitly assumes that the number of competitors is the sole factor determining an individual's best course of action [17,18]. Potential-reproductive-rate arguments based on past investment have long been known to promote flawed conclusions, including the infamous 'Concorde fallacy' [19]. Patterns of investment should be switched if a higher rate of return can be gained elsewhere. To persist stubbornly with the same strategy because of prior investment is as economically irrational as continued development of a plane, such as the Concorde, that will never fly profitably. Evolutionary processes are based on true offspring production and are not expected to follow irrational principles. Female topi are, unlike males, inextricably committed to a prolonged period of parental care, but the resultant potential-reproductive-rate difference does not constrain them to follow false predictions of competition and choosiness.

A better approach is to consider the precise nature of the array of future opportunities that each sex faces. Although these can be altered by past commitments, the logical steps involved still have to be made explicit. The lack of male commitment to parental care is the very reason why

the immediate future brings, with the arrival of a new female, virtually free reproductive opportunities for male topi. The consequent need to use sperm prudently deters males from mating indiscriminately, and the direction of sexual conflict is, therefore, reversed. Similarly, female topi antelopes only have one day to mate. If they cannot delay the opportunity until tomorrow, and benefit from mating with a specific male, it is worthwhile to compete today.

References

1. Clutton-Brock, T.H., and Vincent, A.C.J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature* 351, 58–60.
2. Reynolds, J.D., Goodwin, N.B., and Freckleton, R.P. (2002). Evolutionary transitions in parental care and live bearing in vertebrates. *Phil. Trans. R. Soc. Lond. B* 357, 269–281.
3. Clutton-Brock, T.H., and Parker, G.A. (1992). Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* 67, 437–456.
4. Kokko, H., Jennions, M.D., and Brooks, R.C. (2006). Unifying and testing models of sexual selection. *Ann. Rev. Ecol. Syst.* 37, 43–66.
5. Okuda, N. (1999). Sex roles are not always reversed when the potential reproductive rate is higher in females. *Amer. Nat.* 153, 540–548.
6. Queller, D.C. (1997). Why do females care more than males? *Proc. R. Soc. Lond. B* 264, 1555–1557.
7. Bro-Jørgensen, J. (2007). Reversed sexual conflict in a promiscuous antelope. *Curr. Biol.* 17, 2157–2161.
8. Engqvist, L., and Reinhold, K. (2005). Pitfalls in experiments testing predictions from sperm competition theory. *J. Evol. Biol.* 18, 116–123.
9. Preston, B.T., Stevenson, I.R., Pemberton, J.M., and Wilson, K. (2001). Dominant rams lose out by sperm depletion. *Nature* 409, 681–682.
10. Sæther, S.A., Fiske, P., and Kålås, J.A. (2001). Male mate choice, sexual conflict and strategic

allocation of copulations in a lekking bird. *Proc. R. Soc. Lond. B* 268, 2097–2102.

11. Wilson, J.R., Kuehn, R.E., and Beach, F.A. (1963). Modification in the sexual behaviour of male rats produced by changing the stimulus female. *J. Comp. Physiol. Psychol.* 56, 636–644.
12. Wade, M.J., and Shuster, S.M. (2002). The evolution of parental care in the context of sexual selection: A critical reassessment of parental investment theory. *Am. Nat.* 160, 285–292.
13. Houston, A.I., and McNamara, J.M. (2005). John Maynard Smith and the importance of consistency in evolutionary game theory. *Biol. Philosophy* 20, 933–950.
14. Fromhage, L., McNamara, J.M., and Houston, A.I. (2007). Stability and value of male care for offspring: is it worth only half the trouble? *Biol. Lett.* 3, 234–236.
15. Sogabe, A., and Yanagisawa, Y. (2007). Sex-role reversal of a monogamous pipefish without higher potential reproductive rate in females. *Proc. Roy. Soc. Lond. B* 274, 2959–2963.
16. Forsgren, E., Amundsen, T., Borg, Å.A., and Bjelvenmark, J. (2004). Unusually dynamic sex roles in a fish. *Nature* 429, 551–554.
17. Parker, G.A., and Simmons, L.W. (1996). Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proc. R. Soc. Lond. B* 263, 315–321.
18. Kokko, H., and Monaghan, P. (2001). Predicting the direction of sexual selection. *Ecol. Lett.* 4, 159–165.
19. Dawkins, R., and Carlisle, T.R. (1976). Parental investment, mate desertion and a fallacy. *Nature* 262, 131–133.

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TRP Channels: It's Not the Heat, It's the Humidity

The ability to sense dry or moist air — hygrosensation — is conserved widely, but the underlying mechanisms are obscure. A recent study has shown that TRP channels are required for hygrosensation in *Drosophila*, further expanding the repertoire of sensory modalities mediated by TRP channels.

Craig Montell

As we all know, humidity can have quite an impact on our comfort. When it is low for an extended period, our eyes, skin and nasal passages may become excessively dry. High humidity can also be unpleasant, particularly in combination with hot or cold temperatures. Some people suffering

from rheumatoid arthritis are especially sensitive to high humidity, as many arthritis sufferers report increased pain when the humidity rises [1].

Preferences for one level of humidity over another occur throughout the animal kingdom, and have been documented in worms, flies and a variety of mammals [2–4]. Despite the universality of humidity

sensation — hygrosensation — very little is known concerning the mechanism. In particular, what are the molecules involved in sensing changes in humidity, the putative hygrosensors? Welsh and colleagues [5] have now reported evidence that Transient Receptor Potential (TRP) channels are required in the fruitfly, *Drosophila melanogaster*, for the detection of both dry and moist air [5]. The demonstration that TRP channels are required for hygrosensation adds a new and fascinating wrinkle to the established theme that TRP channels are global detectors of sensory input, ranging from hot and cold temperatures to light, tastants, pheromones, touch, and environmental chemicals [6].