

### Future perspectives

A large number of key players that associate with and regulate integrin-based adhesion complexes have been identified. Due to the molecular complexity and context dependence of cell adhesion, however, a comprehensive understanding of the protein networks involved has yet to be achieved. Recent advances in the isolation and proteomic analysis of adhesion complexes have demonstrated the potential of mass spectrometry-based proteomic approaches to enable global analyses of adhesion receptor-mediated processes. Such approaches, in combination with advanced microscopy, genomic sequencing and computational modelling, will ultimately pave the way to a quantitative, systems-level understanding of adhesion signalling.

### Further reading

- Caswell, P.T., Vadrevu, S., and Norman, J.C. (2009). Integrins: masters and slaves of endocytic transport. *Nat. Rev. Mol. Cell Biol.* 10, 843–853.
- del Pozo, M.A., Alderson, N.B., Kiosses, W.B., Chiang, H.H., Anderson, R.G., and Schwartz, M.A. (2004). Integrins regulate Rac targeting by internalization of membrane domains. *Science* 303, 839–842.
- Geiger, B., Bershadsky, A., Pankov, R., and Yamada, K.M. (2001). Transmembrane crosstalk between the extracellular matrix and the cytoskeleton. *Nat. Rev. Mol. Cell Biol.* 2, 793–805.
- Gupton, S.L., and Waterman-Storer, C.M. (2006). Spatiotemporal feedback between actomyosin and focal-adhesion systems optimizes rapid cell migration. *Cell* 125, 1361–1371.
- Humphries, J.D., Byron, A., and Humphries, M.J. (2006). Integrin ligands at a glance. *J. Cell Sci.* 119, 3901–3903.
- Humphries, J.D., Byron, A., Bass, M.D., Craig, S.E., Pinney, J.W., Knight, D., and Humphries, M.J. (2009). Proteomic analysis of integrin-associated complexes identifies RCC2 as a dual regulator of Rac1 and Arf6. *Sci. Signal.* 2, ra51.
- Morgan, M.R., Humphries, M.J., and Bass, M.D. (2007). Synergistic control of cell adhesion by integrins and syndecans. *Nat. Rev. Mol. Cell Biol.* 8, 957–969.
- Parsons, J.T., Horwitz, A.R., and Schwartz, M.A. (2010). Cell adhesion: integrating cytoskeletal dynamics and cellular tension. *Nat. Rev. Mol. Cell Biol.* 11, 633–643.
- Vogel, V., and Sheetz, M.P. (2009). Cell fate regulation by coupling mechanical cycles to biochemical signaling pathways. *Curr. Opin. Cell Biol.* 21, 38–46.
- Zaidel-Bar, R., Itzkovitz, S., Ma'ayan, A., Lyengar, R., and Geiger, B. (2007). Functional atlas of the integrin adhesome. *Nat. Cell Biol.* 9, 858–867.
- Zamir, E., Katz, M., Posen, Y., Erez, N., Yamada, K.M., Katz, B.Z., Lin, S., Lin, D.C., Bershadsky, A., Kam, Z., and Geiger, B. (2000). Dynamics and segregation of cell-matrix adhesions in cultured fibroblasts. *Nat. Cell Biol.* 2, 191–196.

<sup>1</sup>Wellcome Trust Centre for Cell-Matrix Research, Faculty of Life Sciences, University of Manchester, Manchester M13 9PT, UK.

\*These authors contributed equally to this work.

<sup>†</sup>E-mail: martin.humphries@manchester.ac.uk

## Correspondence

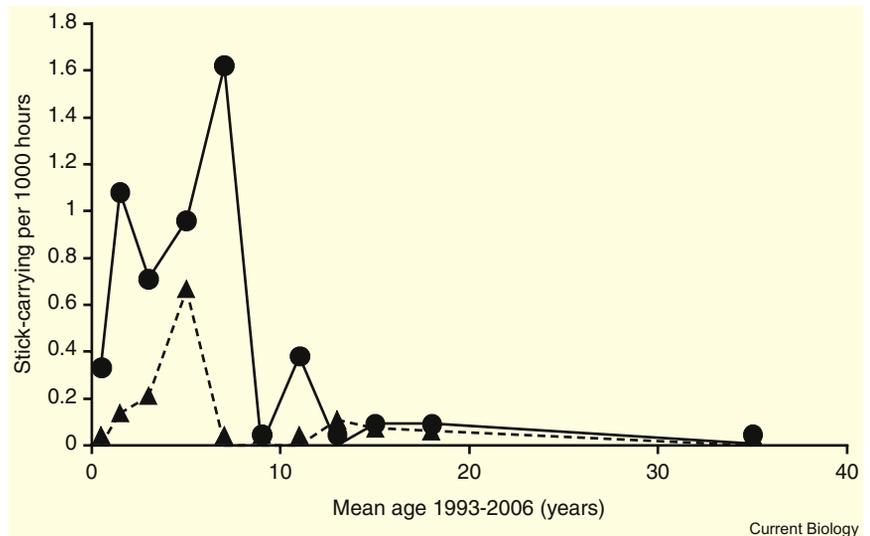
# Sex differences in chimpanzees' use of sticks as play objects resemble those of children

Sonya M. Kahlenberg<sup>1</sup>  
and Richard W. Wrangham<sup>2,\*</sup>

Sex differences in children's toy play are robust and similar across cultures [1,2]. They include girls tending to play more with dolls and boys more with wheeled toys and pretend weaponry. This pattern is explained by socialization by elders and peers, male rejection of opposite-sex behavior and innate sex differences in activity preferences that are facilitated by specific toys [1]. Evidence for biological factors is controversial but mounting. For instance, girls who have been exposed to high fetal androgen levels are known to make relatively

masculine toy choices [3]. Also, when presented with sex-stereotyped human toys, captive female monkeys play more with typically feminine toys, whereas male monkeys play more with masculine toys [1]. In human and nonhuman primates, juvenile females demonstrate a greater interest in infants, and males in rough-and-tumble play. This sex difference in activity preferences parallels adult behavior and may contribute to differences in toy play [1]. Here, we present the first evidence of sex differences in use of play objects in a wild primate, in chimpanzees (*Pan troglodytes*). We find that juveniles tend to carry sticks in a manner suggestive of rudimentary doll play and, as in children and captive monkeys, this behavior is more common in females than in males.

During 14 years of observation of the Kanyawara chimpanzee community in Kibale National Park, Uganda, we found that chimpanzees used sticks in four main ways: as probes to investigate holes potentially containing water or honey; during aggression, either as props in displays or as weapons (throwing or hitting) in aggression



**Figure 1.** Age and sex differences in the rate of stick-carrying in chimpanzees. Females: circles, solid line. Males: triangles, dashed line. Age categories referred to in the main text are infants (0–4.9 years (yrs)), juveniles (5–7.9 yrs), adolescents (8–14.9 yrs), and adults (>15 yrs, male; after full sexual swelling, females). To control for age and satisfy small samples of individuals per age category, each individual was assigned to one of 11 age-classes. Assignment to age-class was determined by the individual's mean age between their start and end of observations, 1993–2006. Age-classes, together with sample sizes of females and males, respectively (total 37 females, 31 males), were: 0–1 yr (1,2), 1–2 yrs (5,4), 2–4 yrs (1,5), 4–6 yrs (3,2), 6–8 yrs (4,1), 8–10 yrs (1,2), 10–12 yrs (1,1), 12–14 yrs (1,1), 14–16 yrs (4,1), 16–20 yrs (2,1) and >20 yrs (14,11). Mean stick-carrying rates across individuals were higher for females than for males (Wilcoxon signed-rank  $T = 3$ ;  $n = 10$  age-classes,  $P = 0.017$  (2-tailed)). No stick-carrying was observed for individuals in the 8–10 year age-class. Note that although the figure shows stick-carrying by individuals whose mid-point was in the adult range, no female carried a stick after becoming a mother.

towards conspecifics or other species; during solitary or social play; and in a behavior we term 'stick-carrying'. Stick-carrying consisted of holding or cradling detached sticks (median length, 36 cm; median weight, 112 g;  $n = 6$  recovered sticks). The juveniles carried pieces of bark, small logs or woody vine, with their hand or mouth, underarm or, most commonly, tucked between the abdomen and thigh (Supplemental information). Individuals carried sticks for periods of one minute to more than four hours during which they rested, walked, climbed, slept and fed as usual. From all-events recording in chimpanzee parties from 1993 to 2006 we found that stick-carrying represented 38.9% of total stick use observations ( $n = 301$ ), and 10.0% of object use observations ( $n = 1170$ ). Regular stick-carrying has no discernible function and has not been reported from other chimpanzee studies [4], even where stick use has been carefully documented for many years [5].

The frequency of stick-carrying peaked among juveniles and was higher in females than males (Figure 1). This sex difference could not be explained by a general propensity for females to use objects more than males [6], because several types of object use were in fact male-biased, including weapon use by adolescents and adults (medians per 1000 hours: male 0.09,  $n = 19$ ; female 0.00,  $n = 30$ ; Mann-Whitney  $U = 597$ ,  $P = 0.002$ , 2-tailed) and use of leaves by adults for wiping their bodies, particularly for cleaning genitals after copulation (male 0.87,  $n = 14$ ; female 0.00,  $n = 24$ ;  $U = 344$ ,  $P = 0.0002$ ).

Probing, by contrast, showed a similar age-sex distribution to stick-carrying, with juvenile and adolescent females using probes more often than same-aged males (male 0.00,  $n = 13$ ; female 0.48,  $n = 10$ ;  $U = 108.5$ ,  $P = 0.004$ ; adults: male 0.00,  $n = 14$ ; female 0.00,  $n = 24$ ;  $U = 182.0$ ,  $P =$  not significant (n.s.)). However individual differences in the frequency of probing and stick-carrying were not correlated (Spearman  $R = 0.20$ ,  $n = 10$  juvenile and adolescent females,  $P =$  n.s.) and there was no overlap in the diameters of carried sticks and probes: carried sticks (range 2–7 cm diameter,  $n = 6$ ) were at least twice as thick as probes (0.3–1 cm,  $n = 14$ ; Supplemental Information). There was thus no evidence of stick-carrying being

motivationally or functionally related to probing.

We suggest instead that sex differences in stick-carrying are related to a greater female interest in infant care, with stick-carrying being a form of play-mothering (i.e. carrying sticks like mother chimpanzees carrying infants). Several lines of evidence support this hypothesis. First, in the few instances when we observed adult females carrying sticks (five females, six events), the behavior always occurred prior to the female's first birth. Thus, unlike probing and other object use, stick-carrying ceased with motherhood. Second, unlike other types of stick use, carried sticks were regularly taken into day-nests (on at least 25 occasions; six females, two males) where individuals rested and were sometimes seen to play casually with the stick in a manner that evoked maternal play. Third, the capacity for young chimpanzees to direct care towards objects has been reported in apes raised by humans [2] and is indicated by two detailed reports from the wild of chimpanzees treating sticks like dolls. At Kanyawara, an 8-year-old male carried and played with a small log for four hours and also made a separate nest for it [7]; and an 8-year-old female at Bossou (Guinea) carried a log, including patting it like "slapping the back of an infant", while her mother was carrying her sick infant sibling [8].

Given that regular stick-carrying has not been reported outside Kanyawara, a social learning component appears important. In Gombe, Tanzania, sex differences among juvenile chimpanzees in the frequency and efficacy of termite-fishing tool use resulted from females modeling their mother's behavior more effectively than males did [9]. A similar effect could possibly account for the sex difference in probing frequency among juveniles at Kanyawara. By contrast, sex differences in juvenile stick-carrying did not result from females observing their mothers carrying sticks, since mothers never carried sticks. Instead, youngsters apparently learned socially from each other. Such juvenile traditions have previously been described only in humans [10]. The sex difference in stick-carrying in juvenile Kanyawara chimpanzees arises without any teaching by adults and is consistent with practice for adult roles. Our findings suggest that a similar sex difference could have

occurred in the human and pre-human lineage at least since our common ancestry with chimpanzees, well before direct socialization became an important influence.

#### Supplemental Information

Supplemental Information includes experimental procedures as well as two supplemental figures and can be found with this article online at doi: 10.1016/j.cub.2010.11.024.

#### Acknowledgments

Research was supported by NSF awards 9807448 and 0416125, Leakey Foundation, National Geographic Society, Getty Foundation, and Wenner-Gren Foundation. In Uganda we thank UWA and MUBFS for permission, and E. Otali, G. Basata, C. Chapman, K. Duffy, M. Emery Thompson, I. Gilby, C. Hooven, J. Kasenene, M. Muller, A. Pokempner and M. Wilson for assistance. For fieldwork we thank the late J. Barwogeza, the late J. Basigara, D. Kateeba, C. Katongole, F. Mugurusi, the late D. Muhangyi, the late C. Muruuli, S. Musana, D. Sebugwawo, and P. Tuhairwe. For comments we thank J. Benenson, M. Emery Thompson, T. Humle, M. Hines, M. Muller, W. McGrew, B. O'Connor and three reviewers.

#### References

1. Hassett, J.M., Siebert, E.R., and Wallen, K. (2008). Sex differences in rhesus monkey toy preferences parallel those of children. *Hormones Behav.* 54, 359–364.
2. Pellegrini, A.D. and Smith, P.K. (2005). *The Nature of Play: Great Apes and Humans* (New York: Guilford Press).
3. Pasterski, V.L., Geffner, M.E., Brain, C., Hindmarsh, P., Brook, C., and Hines, M. (2005). Prenatal hormones and postnatal socialization by parents as determinants of male-typical toy play in girls with congenital adrenal hyperplasia. *Child Dev.* 76, 264–278.
4. Whiten, A., Goodall, J., McGrew, W.C., Toshisada, N., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., and Boesch, C. (1999). Chimpanzee cultures. *Nature* 399, 682–685.
5. Humle, T. (in press). The tool use repertoire of Bossou chimpanzees. In *The Chimpanzees of Bossou and Nimba*, T. Matsuzawa, T. Humle and Y. Sugiyama, eds. (Tokyo: Springer-Verlag).
6. Boesch, C., and Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54, 86–99.
7. Wrangham, R.W., and Peterson, D. (1996). *Demonic Males: Apes and the Origins of Human Violence* (Boston: Houghton Mifflin).
8. Matsuzawa, T. (1997). The death of an infant chimpanzee at Bossou, Guinea. *Pan Africa News* 4, 4–6.
9. Lonsdorf, E.V., Eberly, L.E., and Pusey, A.E. (2004). Sex differences in learning in chimpanzees. *Nature* 428, 715–716.
10. Opie, I., and Opie, P. (1969). *Children's Games in Street and Playground* (Oxford: Oxford University Press).

<sup>1</sup>Department of Biology, Bates College, Lewiston, Maine 04240, USA. <sup>2</sup>Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA.

\*E-mail: wrangham@fas.harvard.edu