Animal behaviour: task differentiation by personality in spider groups

Article (Published Version)

15. Marcet, B., Chevalier, B., Luxardi, G., Coraux, C., Zaragosi, L.E., Cibois, M., Robbe-Sermesant, K., Jolly, T., Cardinaud, B., Moreilhon, C., *et al*. (2011). Control of vertebrate multiciliogenesis by miR-449 through direct repression of the Delta/Notch pathway. Nat. Cell Biol. *13*, 693–699.
16. Song, R., Walentek, P., Sponer, N., Klimke, A., Lee, J.S., Dixon, G., Harland, R., Wan, Y., Lishko, P., Lize, M., *et al*. (2014). miR-34/449 miRNAs are required for motile ciliogenesis by repressing cp110. Nature *510*, 115–120.
17. Wallmeier, J., Al-Mutairi, D.A., Chen, C.T., Loges, N.T., Pennekamp, P., Menchen, T., Ma, L., Shamseldin, H.E., Olbrich, H., Dougherty, G.W., *et al*. (2014). Mutations in CCNO result in congenital mucociliary clearance disorder with reduced generation of multiple motile cilia. Nat. Genet. *46*, 646–651.
18. Boon, M., Wallmeier, J., Ma, L., Loges, N.T., Jaspers, M., Olbrich, H., Dougherty, G.W., Raidt, J., Werner, C., Amirav, I., *et al*. (2014). MCIDAS mutations result in a mucociliary clearance disorder with reduced generation of multiple motile cilia. Nat. Commun. *5*, 4418.
19. Chen, Z., Indjeian, V.B., McManus, M., Wang, L., and Dynlacht, B.D. (2002). CP110, a cell cycle-dependent CDK substrate, regulates centrosome duplication in human cells. Dev. Cell *3*, 339–350.
20. Spektor, A., Tsang, W.Y., Khoo, D., and Dynlacht, B.D. (2007). Cep97 and CP110 suppress a cilia assembly program. Cell *130*, 678–690.

Swiss Institute for Experimental Cancer Research (ISREC), School of Life Sciences, Swiss Federal Institute of Technology (EPFL), Lausanne, Switzerland.
*E-mail: pierre.gonczy@epfl.ch

http://dx.doi.org/10.1016/j.cub.2014.07.006

Animal Behaviour: Task Differentiation by Personality in Spider Groups

In social animals, group efficiency is often assumed to increase with task differentiation, but this requires that individuals are better than generalists at the task they specialize in. A new study finds that individual *Anelosimus studiosus* spiders do predominantly perform the task they excel at, in line with their individual personality type, when they are placed in groups.

Lena Grinsted* and Jonathan P. Bacon

Did you think that all spiders are ferocious predators, which attack any other spider or bug they come across? Well, think again. Sure, it is true that many spiders will eat their own offspring if they get in the way, and yes, some females will happily snack on their partners during mating. But some spiders form cooperative communities where they live peacefully side by side [1]. Darwin himself expressed surprise when he came across a group-living spider in 1832 (*Parawixia bistriata*) [2]. One spider that facultatively forms small groups is *Anelosimus studiosus*. Within an *Anelosimus studiosus* group some females show an aggressive personality type and participate more in colony defense and prey capture, while others are docile and engage more in brood care [3]. Experimental groups containing a mix of these two different personalities outperform groups of only one personality type, using egg-case weight as a proxy for fitness [4]. An elegant new study by Colin M. Wright and colleagues [5] has found the reason why. Aggressive females are simply more efficient at foraging, web construction and defense, while docile females excel at raising the young. Hence, when groups contain a mix of both types, emergent task differentiation increases overall group performance benefitting all group members.

Consider a leafcutter ant nest. Some worker ants are tiny, while others are huge. It is easy to imagine how an ant colony can benefit from this extreme polymorphism; tiny workers will efficiently feed and clean the fungus gardens, while large soldiers with gigantic mandibles are superior at defending the nest against larger predators [6]. Task specialization accompanied by polymorphism leads to more efficient and successful groups. Why task differentiation would be beneficial within societies of cooperative breeders that lack morphological castes, such as the social spiders, birds and mammals, is harder to imagine. For example, why do helpers in the cooperatively breeding noisy miner, *Manorina melanocephala*, often specialize in either chick provisioning or mobbing nest predators, rather than participating equally in all tasks [7]? Individuals within these types of social groups are all morphologically capable of performing any task. So why do some group members engage in riskier activities, such as colony defense, more than others?

Perhaps some individuals are just inherently better than others at certain tasks, or they become better over time with more practice [8]. If, at the same time, other group members are, or become better at other tasks, and individuals mostly perform the tasks they are good at, each group member may gain the benefits of improved group efficiency. For example, in the cooperatively breeding cichlid fish *Neolamprologus pulcher*, task participation varies with body size and age, perhaps because smaller fish are better at defending the nest while larger fish are better at removing sand from the nest [9]. However, the assumption that task participation actually correlates with individual task performance in non-polymorphic social animals has rarely been proven.

Social spiders provide a good example of highly cooperative societies in which female group members are non-polymorphic and yet show reproductive skew and task differentiation within groups [10,11]. Only about 25 species bear the title 'social' out of almost 45,000 spider species described [12]. These are cooperative breeders that live in extremely inbred societies. In the evolution of permanent sociality from subsociality, a pre-mating dispersal stage has been lost, leaving brothers and sisters to mate generation after generation (within-group relatedness: $r > 0.5$ [13]). Subsocial species, such as *A. studiosus*, show cooperation at the juvenile stage, after which siblings disperse to breed alone, maintaining an outbred mating system [1]. The new findings by Wright *et al.* [5] showing that *A. studiosus* specialize on tasks they are efficient at when placed in groups may be key to understanding why social spiders show individual behavioral variation.

Figure 1. Social spiders.
Six *Stegodyphus sarasinorum* attack an ant prey, while their more timid nestmates (not shown) remain in the safety of the nest. (Photo: Virginia Settepani.)

In some Amazonian social spiders, such as *Anelosimus eximius* [11], task differentiation is age related, as individuals acquire more colony tasks with age, while in Old World social spiders, something more intriguing is going on. Despite being genetically highly similar and all of similar age and developmental stage, *Stegodyphus sarasinorum* spiders (Figure 1) show task differentiation in prey attack: certain individuals specialize in bringing in the food while others rarely or never help out [11]. What is it that predicts differential participation in this spider? Individual personality is the answer, with personality defined as behavioral differences among individuals that are consistent over time and across context [10]. Individuals vary in their level of boldness, and bolder spiders specialize in prey attack. What do the shy group members then do? And are the bold group members actually better at catching prey? These are still unanswered questions in social species, but perhaps the behavioral strategy of doing what you are good at, now demonstrated so clearly in the subsocial *A. studiosus* [5], provides the answer.

A. studiosus is a model organism for studies on animal personality and by far the best-studied spider in the research area of behavioral types. Interestingly, instead of showing gradual, normally distributed individual personality scores, this spider shows a bimodal distribution [14]. This allows researchers to group individual spiders into aggressive and docile phenotypes, and it turns out that different personality traits are correlated in a behavioral syndrome [15]. Aggressive individuals show shorter latencies to attack prey and to resume movement after a disturbance, and prefer to position themselves further from conspecifics in forced pairings in the lab. The docile phenotypes show the opposite trends in all of the above personality tests.

A. studiosus is usually found living solitarily in nature. A small percentage of nests, however, contain multiple females with an average of about five females per nest. In its usual habitat in the U.S. the proportion of multi-female nests varies from 0 to 15% [14]. Groups of adult females probably stem from young failing to disperse from their maternal nest, and relatedness within groups is therefore at the half-sib level ($r \sim 0.25$) [16]. Females may share prey, and it seems they do not discriminate their own and foreign egg cases and offspring, but they lack the features of reproductive skew and tolerance, which are characteristic of social cooperative breeders. All females within the groups reproduce and mothers will aggressively chase away other adult group members [17]. Hence, *A. studiosus* is a subsocial species that sometimes occurs in groups. This makes it an ideal species for studies on the costs and benefits of group living, as group sizes are easily manipulated in the lab.

Studies asking whether behavioral variation is an adaptation to sociality are now needed in fully social spider species. All populations of *A. studiosus* studied to date have contained a mix of aggressive and docile phenotypes [15], personality traits have been found to be heritable [18], and group forming behavior is non-plastic in solitary populations [14]. Therefore, different personalities are maintained even in populations that exist purely of solitary spiders with no behavioral plasticity to naturally form groups. Thus, it seems unlikely that mixed phenotypes is an adaptation to group living or sociality in this species.

Consistent personalities and behavioral syndromes have been documented in a diverse range of both social and non-social species, including insects, spiders, fish, birds and mammals [19]. Behavioral differences may occur in some species due to stochasticity and differences in internal states and may be adaptive in others due, for example, to frequency-dependent selection [20]. If personalities exist in a non-social or subsocial ancestral state, whether it be maintained stochastically or through selection, and if phenotypic variation within groups proves beneficial in the transition to sociality, selection might quickly amplify individual differences. Hence, if having mixed personalities within a group provides adaptive benefits in the form of improved group performance, this mechanism behind task specialization might be prevalent in a whole range of other non-polymorphic cooperative breeders. This is an exciting era for research on social organization in cooperative animals, a field previously dominated by studies on eusocial insects. The question remains whether personality is a common mechanism behind task allocation across taxa, and whether social spiders, and other cooperative breeders, have adaptively employed this mechanism.

References

1. Lubin, Y., and Bilde, T. (2007). The evolution of sociality in spiders. Adv. Study Behav. *37*, 83–145.
2. Darwin, C. (1845). The Voyage of the Beagle. Journal of Reasearches into the Natural History and Geology of the Countries Visited During the Voyage of HMS Beagle Round the World (London: J. Murray).
3. Pruitt, J.N., and Riechert, S.E. (2011). Within-group behavioral variation promotes biased task performance and the emergence of a defensive caste in a social spider. Behav. Ecol. Sociobiol. *65*, 1055–1060.
4. Pruitt, J.N., and Riechert, S.E. (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. Proc. R. Soc. B. Biol. Sci. *278*, 1209–1215.
5. Wright, C.M., Holbrook, C.T., and Pruitt, J.N. (2014). Animal personality aligns task specialization and task proficiency in a spider society. Proc. Natl. Acad. Sci. USA *111*, 9533–9537.
6. Wilson, E.O. (1953). The origin and evolution of polymorphism in ants. Quart. Rev. Biol. *28*, 136–156.
7. Arnold, K.E., Owens, I.P.F., and Goldizen, A.W. (2005). Division of labour within cooperatively breeding groups. Behaviour *142*, 1577–1590.
8. Gordon, D.M. (1996). The organization of work in social insect colonies. Nature *380*, 121–124.
9. Bruintjes, R., and Taborsky, M. (2011). Size-dependent task specialization in a cooperative cichlid in response to experimental variation of demand. Anim. Behav. *81*, 387–394.
10. Grinsted, L., Pruitt, J.N., Settepani, V., and Bilde, T. (2013). Individual personalities shape task differentiation in a social spider. Proc. R. Soc. B. Biol. Sci. *280*.
11. Settepani, V., Grinsted, L., Granfeldt, J., Jensen, J.L., and Bilde, T. (2013). Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). J. Evol. Biol. *26*, 51–62.
12. Avilés, L. (1997). Causes and consequences of cooperation and permanent-sociality in spiders. In The Evolution of Social Behavior in Insects and Arachnids, J.C. Choe and B.J. Crespi, eds. (Cambridge, United Kingdom: Cambridge University Press), pp. 476–498.
13. Johannesen, J., Hennig, A., Dommermuth, B., and Schneider, J.M. (2002). Mitochondrial DNA distributions indicate colony propagation by single matri-lineages in the social spider *Stegodyphus dumicola* (Eresidae). Biol. J. Linn. Soc. *76*, 591–600.
14. Riechert, S.E., and Jones, T.C. (2008). Phenotypic variation in the social behaviour of the spider *Anelosimus studiosus* along a latitudinal gradient. Anim. Behav. *75*, 1893–1902.
15. Pruitt, J.N., Riechert, S.E., Iturralde, G., Vega, M., Fitzpatrick, B.M., and Aviles, L. (2010). Population differences in behaviour are explained by shared within-population trait correlations. J. Evol. Biol. *23*, 748–756.
16. Duncan, S.I., Riechert, S.E., Fitzpatrick, B.M., and Fordyce, J.A. (2010). Relatedness and genetic structure in a socially polymorphic population of the spider *Anelosimus studiosus*. Mol. Ecol. *19*, 810–818.
17. Furey, F.E. (1998). Two cooperatively social populations of the theridiid spider *Anelosimus studiosus* in a temperate region. Anim. Behav. *55*, 727–735.
18. Pruitt, J.N., and Riechert, S.E. (2009). Sex matters: sexually dimorphic fitness consequences of a behavioural syndrome. Anim. Behav. *78*, 175–181.
19. Bell, A.M., Hankison, S.J., and Laskowski, K.L. (2009). The repeatability of behaviour: a meta-analysis. Anim. Behav. *77*, 771–783.
20. Dall, S.R.X., Houston, A.I., and McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol. Lett. *7*, 734–739.

Evolution, Behaviour and Environment Group, School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK.
*E-mail: l.grinsted@sussex.ac.uk

http://dx.doi.org/10.1016/j.cub.2014.07.008

Dinosaur Evolution: Feathers Up for Selection

A new specimen of the early bird *Archaeopteryx* shows remarkable plumage preservation, including pennaceous leg feathers. But whether birds went through a four-winged stage, and in what exact functional context feathers evolved remains a matter of debate.

Zhonghe Zhou

After nearly one and half century of study and debate on whether extant birds are descendants of dinosaurs, paleontologists now generally agree that all birds are derived from a group of small-sized theropods (a suborder of bipedal saurischian or 'lizard-hipped' dinosaurs). In the past two decades, paleontology has also made remarkable progress in understanding of the origin and early evolution of bird feathers. Since the first report of proto-feathers from the theropod dinosaur *Sinosauropteryx* [1], diverse types of feathers in dinosaurs, including theropods and ornithischians, (one of the two basic divisions of dinosaurs, the 'bird-hipped' dinosaurs) have been reported mainly from the Early Cretaceous (about 120 million years ago) but also Middle-Late Jurassic (about 160 million years ago) deposits in northeastern China that have tremendously improved our understanding of the evolutionary transition from dinosaur to bird [1–4]. More recently, evidence of the color of fossil feathers in the form of preserved melanosomes has been found in various dinosaurs and early birds, providing evidence of their appearance and inferred behaviors [5–7]. This further allowed new investigations into the details of feather morphology and their functional explanations in these new taxa as well as rekindled studies on previously known birds, such as the well-known *Archaeopteryx lithographica* [8–10]. Many of our traditional views on the origin and early evolution of bird feathers have since been revolutionized; we now know that feathers are not restricted to birds, but are also found in some non-avian dinosaurs; also, they probably did not originally evolve for flight, but rather in some other functional context such as insulation, display, camouflage etc. There is also support for hypotheses that flapping flight in modern birds most likely evolved through a four-winged stage in dinosaurs. Clearly, feathers are key to understanding the evolutionary forces and events that led to the emergence of flying birds. Now, Foth and colleagues [11] report a new specimen of the iconic early bird *Archaeopteryx* that shows unique preservation of feathers.

Archaeopteryx lithographica, arguably the most studied species in vertebrate paleontology, has long been held as the earliest and most primitive bird, ever since its first skeleton was reported in 1861. Undoubtedly, *Archaeopteryx* has played a key role in the discussion of the origin of birds, feathers, and avian flight. However, with the remarkable discoveries of feathered dinosaurs (*e.g.*, *Anchiornis* and *Xiaotingia*), particularly from the Jurassic lake deposits in northeastern China, even the iconic status of *Archaeopteryx* as the oldest known bird has been challenged [4]. Furthermore, until now, information on the plumage of *Archaeopteryx* (largely limited to the London and Berlin specimens) remained incomplete compared to the exceptional preservation of the plumage in several feathered dinosaurs and early birds from China. The complete articulated 10th