

Chinese is typically characterized by the co-existence of visuospatial and phonological disorders in a dyslexic child. This pattern of behavioral and pathophysiological profiles is different from that in English dyslexia, which is generally associated with a core phonological deficit in the absence of abnormal visual processing [7].

Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01549-8](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01549-8)

Acknowledgments

This work was supported by grants from the Ministry of Science and Technology of China (2005CB522802), National Natural Science Foundation of China (30621004), Research Grants Council of Hong Kong (775709M), and National Institutes of Health (1R01HD056107-01A). We thank A. Chan, D. Dong, Y. Ha, J. Kwok, and J. Yang for assistance.

References

1. Goswami, U. (2006). Neuroscience and education: from research to practice? *Nat. Rev. Neurosci.* 7, 406–413.
2. Turkeltaub, P.E., Gareau, L., Flowers, D.L., Zeffiro, T., and Eden, G. (2003). Development of neural mechanisms for reading. *Nat. Neurosci.* 6, 767–773.
3. Hoefft, F., Meyler, A., Hernandez, A., Juel, C., Taylor-Hill, H., Martindale, J.L., McMillon, G., Kolchugina, G., Black, J.M., Faizi, A., et al. (2007). Functional and morphometric brain dissociation between dyslexia and reading ability. *Proc. Natl. Acad. Sci. USA* 104, 4234–4239.
4. Horwitz, B., Rumsey, J.M., and Donohue, B. C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proc. Natl. Acad. Sci. USA* 95, 8939–8944.
5. Schlaggar, B.L., and McCandliss, B.D. (2007). Development of neural systems for reading. *Annu. Rev. Neurosci.* 30, 475–503.
6. Temple, E., Poldrack, R.A., Salidis, J., Deutsch, G.K., Tallal, P., Merzenich, M.M., and Gabrieli, J.D.E. (2001). Disrupted neural responses to phonological and orthographic processing in dyslexic children: an fMRI study. *NeuroReport* 12, 299–307.
7. Ramus, F., Rosen, S., Dakin, S.C., Day, B.L., Castellote, J.M., White, S., and Frith, U. (2003). Theories of developmental dyslexia: insights from a multiple case study of dyslexic adults. *Brain* 126, 841–865.
8. Siok, W.T., Perfetti, C.A., Jin, Z., and Tan, L.H. (2004). Biological abnormality of impaired reading is constrained by culture. *Nature* 431, 71–76.
9. Siok, W.T., Niu, Z.D., Jin, Z., Perfetti, C.A., and Tan, L.H. (2008). A structural-functional basis for dyslexia in the cortex of Chinese readers. *Proc. Natl. Acad. Sci. USA* 105, 5561–5566.
10. Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., and Shulman, G.L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3, 292–297.

¹State Key Laboratory of Brain and Cognitive Sciences, ²Department of Linguistics, and ³Vice-Chancellor's Office, The University of Hong Kong, Pokfulam Road, Hong Kong, China. ⁴Beijing 306 Hospital, Beijing 100101, China. E-mail: tanlh@hku.hk

Herbivory in a spider through exploitation of an ant–plant mutualism

Christopher J. Meehan^{1,5}, Eric J. Olson², Matthew W. Reudink³, T. Kurt Kyser⁴, and Robert L. Curry¹

Spiders are thought to be strict predators [1]. We describe a novel exception: *Bagheera kiplingi*, a Neotropical jumping spider (Salticidae) that exploits a well-studied ant–plant mutualism, is predominantly herbivorous. From behavioral field observations and stable-isotope analyses, we show that the main diet of this host-specific spider comprises specialized leaf tips (Beltian food bodies; Figure 1A) from *Vachellia* spp. ant-acacias (formerly *Acacia* spp.), structures traded for protection in the plant's coevolved mutualism with *Pseudomyrmex* spp. ants that inhabit its hollow thorns [2]. This is the first report of a spider that feeds primarily and deliberately on plants.

Jumping spiders use advanced color-vision, agility, and cognitive skills to prey upon invertebrates [3]. The Salticidae is the largest family of spiders (>5,000 species), and members of this diverse group employ a broad range of foraging strategies. However, departures from carnivory in salticids — or in any of the 40,000 described spiders — are rare [1]: several cursorial spiders imbibe nectar as an occasional supplement to animal prey [4], and some juvenile orb-weavers incidentally ingest pollen when recycling their webs [5].

We discovered herbivory in *B. kiplingi* during field studies in southeastern Mexico (Quintana Roo, involving *V. collinsii* acacias inhabited by *P. peperii* ants) and northwestern Costa Rica (Guanacaste Province, involving *V. collinsii* and *V. cornigera* inhabited by *P. spinicola*, *P. flavicornis*, or *P. nigrocincta*). Between 2001 and 2008, we systematically observed individual *B. kiplingi* in these two regions to study foraging behavior. We supported direct observations of spiders in Mexico with high-definition videography.

Individuals at both sites fed predominantly on Beltian bodies,

which represented nearly the full diet of spiders in Mexico (91% of items consumed) but relatively less in Costa Rica (60%; $\chi^2 = 14.2$, $df = 3$, $P < 0.05$; Figure 1B). Spiders occasionally supplemented Beltian bodies with extrafloral nectar, another resource central to the ant–acacia mutualism [2]. They also preyed on acacia-ant larvae, small nectar-feeding flies, and (rarely) smaller conspecifics.

We observed focal *B. kiplingi* circumventing the well-known defenses of the acacia's *Pseudomyrmex* ant-inhabitants, which keep the plant free of most herbivores and encroaching vegetation [2]. These spiders occur almost exclusively on ant-occupied acacias, where they breed year-round and generally build their nests at the distal tips of older leaves (86%; $N = 110$) that have low rates of ant patrol (see Supplemental Data available on-line). Foraging *B. kiplingi* actively avoid ant-guards and exhibit situation-specific strategies (for example, changing targets if approached by ants) when harvesting Beltian bodies and when taking nectar or ant larvae (Supplemental Movies S1–S5).

Stable-isotope analyses confirmed *B. kiplingi* herbivory (Figure 1C; see also Supplemental Data). Our results are consistent with other food-web studies: the tissues of herbivores tend to have lower $^{15}\text{N}:^{14}\text{N}$ ratios (expressed as $\delta^{15}\text{N}$) relative to carnivores, whereas consumers tend to match $^{13}\text{C}:^{12}\text{C}$ ratios ($\delta^{13}\text{C}$) of their food [6]. Mexican *B. kiplingi* specimens had $\delta^{15}\text{N}$ profiles averaging 4.8% lower than those of other jumping spiders from surrounding vegetation, but only 2.1% and 2.9% higher than ant workers and Beltian bodies, respectively. *B. kiplingi* spiders and ant workers at this site had $\delta^{13}\text{C}$ signatures virtually identical to those of Beltian bodies, whereas other spiders exhibited $\delta^{13}\text{C}$ values that did not match those of Beltian bodies.

Using dietary mixing models (see Supplemental Data), we estimate that *B. kiplingi* in Mexico ($N = 50$) derive >95% of assimilated C and N from ant-acacias, including $89 \pm 13.2\%$ (mean \pm SE) directly from plant tissue and $8 \pm 7.9\%$ indirectly from acacia-ant larvae. Individuals of all age-sex classes had similar diets, suggesting that spiders in this population are

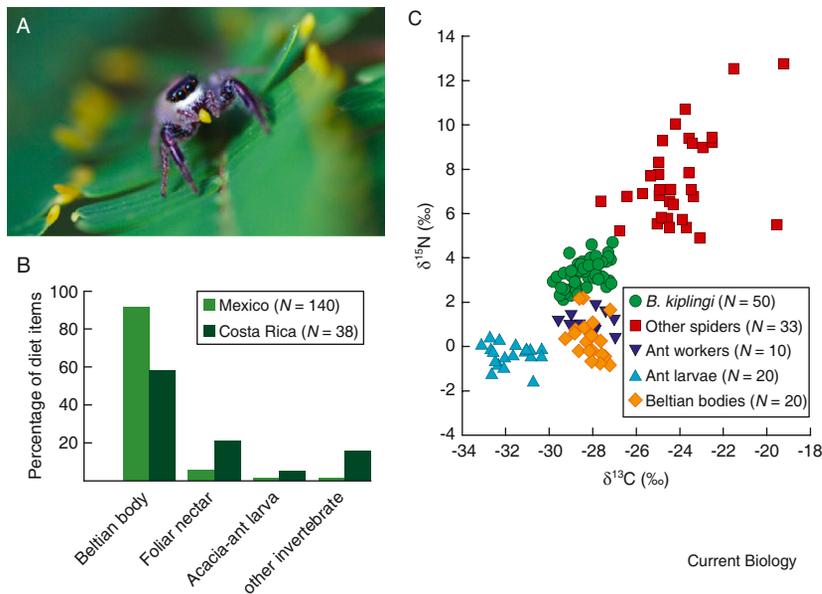


Figure 1. Evidence of herbivory in the jumping spider *Bagheera kiplingi*.

(A) Adult female consumes a Beltian body harvested from the tip of an ant-acacia leaflet. (Photo: M. Milton.) (B) *B. kiplingi* diet estimated from field observations. Beltian bodies contributed more to the spider's diet than did other food sources, especially in Mexico (sample sizes refer to numbers of food items observed). (C) Stable-isotope profiles of Mexican *B. kiplingi* in relation to other study-system components. The scatterplot shows results for each individual (sample sizes in parentheses), highlighting the difference between *B. kiplingi* and other spiders: *Bagheera*'s low $\delta^{15}\text{N}$ profile (a proxy for trophic level) resembles that of an herbivore, whereas overlap with the $\delta^{13}\text{C}$ profiles of Beltian bodies reflects heavy contribution to the spider's assimilated diet.

near-total vegetarians throughout their lives. Analyses of Costa Rican specimens (N = 11) indicated a larger contribution of other animal prey to the diet of spiders there (Supplemental Figure S1), consistent with feeding patterns observed in the field (Figure 1B).

A widespread and intimate distributional association exists between *B. kiplingi* and myrmecophytic *Vachellia* spp. The spider's known geographic range coincides with that of ant-acacia systems throughout Mesoamerica (Figure S2). Hundreds of individual *B. kiplingi* may inhabit a single ant-acacia, yet during a seven-year inventory of all salticids at our Costa Rican site (N = 1174 individuals from 48 species), we observed only two *B. kiplingi* individuals on plants other than *Vachellia* spp. In both Mexico and Costa Rica, we also found nests of *B. kiplingi* (N > 200) only on ant-acacias or adjacent foliage. Reports of host-plant specificity in a spider are rare [7], and no spider has been shown previously to exploit the specific resources exchanged in any mutualism.

Consumption of Beltian bodies by *B. kiplingi* may derive from foraging on other static food sources, such as acacia-ant larvae or eggs of other insects. However, while enriched in sugar and protein, these low-fat food bodies are 80% structural fiber [8] and are thus poor surrogates for animal prey. Given that no other spider is known to feed on vegetation, the digestive physiology of *B. kiplingi* may be specialized to process such a fibrous, nitrogen-poor material [9]. Year-round availability of ant-plant food [2], combined with indirect defensive benefits possibly conferred by the acacia-ants [10], may also help explain how the spider's carnivorous ancestor transitioned to herbivory.

The host-specific natural history of *B. kiplingi* demonstrates that commodities modified for trade in a pairwise mutualism can, in turn, shape the ecology and evolutionary trajectory of other organisms that intercept these resources. Here, one species within an ancient lineage of carnivorous arthropods — the spiders — has achieved herbivory by exploiting plant goods exchanged for animal services. While the advanced

sensory-cognitive functions of salticids [3] may have pre-adapted *B. kiplingi* for harvesting Beltian bodies, this spider's unprecedented trophic shift was contingent upon the seemingly unrelated coevolution between an ant and a plant.

Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01626-1](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01626-1)

Acknowledgments

We thank K. Arakawa, M. Milton and J. LaPergola (field assistance); G.S. Bodner and W.K. Maddison, and P.S. Ward (specimen identification); R. Michener, K. Klassen, and A. Vuletich (lab assistance); Centro Ecológico Akumal and Guanacaste Conservation Area (logistical support); and J.L. Bronstein, N.K. Whiteman, D.J. Kronauer, and N.E. Pierce (manuscript comments). This research was funded in part by the Animal Behavior Society, Sigma Xi, Villanova University, and the Earthwatch Institute.

References

1. Foelix, R.F. (1996). *Biology of Spiders*, 2nd Edition, (New York: Oxford University Press).
2. Janzen, D.H. (1966). Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20, 249–275.
3. Harland, D.P., and Jackson, R.R. (2000). 'Eight-legged cats' and how they see — a review of recent research on jumping spiders (Araneae: Salticidae). *Cimbebasia* 16, 231–240.
4. Jackson, R.R., Pollard, S.D., Nelson, X.J., Edwards, G.B., and Barrion, A.T. (2001). Jumping spiders (Araneae: Salticidae) that feed on nectar. *J. Zool.* 255, 25–29.
5. Smith, R.B., and Mommson, T.P. (1984). Pollen feeding in an orb-weaving spider. *Science* 226, 1330–1332.
6. Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718.
7. Romero, G.Q., Mazzafera, P., Vasconcellos-Neto, J., and Trivelin, P.C.O. (2006). Bromeliad-living spiders improve host plant nutrition and growth. *Ecology* 87, 803–808.
8. Heil, M., Baumann, B., Krüger, R., and Linsenmair, K.E. (2004). Main nutrient compounds in food bodies of Mexican *Acacia* ant-plants. *Chemoecology* 14, 45–52.
9. Denno, R.F., and Fagan, W.F. (2003). Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84, 2522–2531.
10. Bernays, E., and Graham, M. (1988). On the evolution of host specificity in phytophagous arthropods. *Ecology* 69, 886–892.

¹Department of Biology, Villanova University, Villanova, PA 19085, USA. ²Heller School for Social Policy and Management, Brandeis University, Waltham, MA 02454, USA.

³Department of Forensic Science, Trent University, Peterborough, ON K9J 7B8, Canada ⁴Department of Geological Sciences and Geological Engineering, Queen's University, Kingston, ON K7L 3N6, Canada. ⁵Present address: Department of Ecology & Evolutionary Biology, University of Arizona, P.O. Box 210088, Tucson, AZ 85721, USA.

E-mail: meehan.christopher@gmail.com