

sory, and premotor areas (17, 20, 21), and neurons in this region integrate visual, tactile, and proprioceptive information from the hand (15, 16, 21–26). People with parietal lesions sometimes show an inability to identify their own limbs as part of the body (1). This could reflect impaired multisensory integration of body-related information. However, it is still somewhat unclear whether the activity in the intraparietal cortex reflects the feeling of ownership per se, because we only detected a trend for illusion-related activity in this region (interaction effect, $-45, -54, 57$; $P < 0.009$).

The elicitation of the rubber hand illusion depends on the integration of visual and tactile information and the resolution of differences between the visual and position sense representations. The period before the illusion develops is critical in this respect, and it probably involves a recalibration of position sense for the hand (5). Before the illusion started, we found increased levels of activity in the bilateral intraparietal cortex, bilateral dorsal premotor cortex, and supplementary motor area, as well as the left cerebellum, left putamen, and left ventral thalamus (Fig. 4) (table S3). Several of these areas are known to be involved in the processing of proprioceptive signals as revealed by tendon vibration experiments (27). Likewise, some of the areas are involved in arm reaching in humans and nonhuman primates (20, 28–30). Thus, the recalibration of limb position in a reaching circuit might be a key mechanism for the elicitation of the illusion, and indeed experiencing the illusion has behavioral consequences for arm movements. After having experienced the rubber hand illusion of their left hand, subjects make a reaching error (toward the location of the rubber hand) when asked to point toward their hidden left hand (5, 31).

In summary, the rubber hand illusion depends on three neural mechanisms: multisensory integration in parietocerebellar regions, recalibration of proprioceptive representations of the upper limb in a reaching circuit, and self-attribution in the premotor cortex (8). Our results associate activity in the premotor cortex with the feeling of ownership of a seen limb, and we suggest that multisensory integration in a body-centered reference frame is the underlying mechanism of self-attribution.

References and Notes

- M. Critchley, *The Parietal Lobes* (Edward Arnold, London, 1953).
- M. Critchley, *Mt. Sinai J. Med.* **41**, 82 (1974).
- T. E. Feinberg, *Semin. Neurol.* **17**, 129 (1997).
- K. J. Meador, D. W. Loring, T. E. Feinberg, G. P. Lee, M. E. Nichols, *Neurology* **55**, 816 (2000).
- M. Botvinick, J. Cohen, *Nature* **391**, 756 (1998).
- K. C. Armel, V. S. Ramachandran, *Proc. R. Soc. London Ser. B* **270**, 1499 (2003).
- F. Pavani, C. Spence, J. Driver, *Psychol. Sci.* **11**, 353 (2000).
- See supporting data at Science Online.
- R. W. Mitchell, in *The Self: From Soul to Brain*, J. LeDoux, Ed. (New York Academy of Sciences, New York, 2003), pp. 39–62.
- L. E. Bahrick, J. S. Watson, *Dev. Psychol.* **21**, 963 (1985).
- E. van den Bos, M. Jeannerod, *Cognition* **85**, 177 (2002).
- M. S. Graziano, G. S. Yap, C. G. Gross, *Science* **266**, 1054 (1994).
- M. S. Graziano, X. T. Hu, C. G. Gross, *J. Neurophysiol.* **77**, 2268 (1997).
- M. S. Graziano, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 10418 (1999).
- M. S. Graziano, D. F. Cooke, C. S. Taylor, *Science* **290**, 1782 (2000).
- D. M. Lloyd, D. I. Shore, C. Spence, G. A. Calvert, *Nature Neurosci.* **6**, 17 (2003).
- G. Rizzolatti, G. Luppino, M. Matelli, *Electroencephalogr. Clin. Neurophysiol.* **106**, 283 (1998).
- G. Rizzolatti, C. Scandolara, M. Matelli, M. Gentilucci, *Behav. Brain Res.* **2**, 125 (1981).
- G. Rizzolatti, C. Scandolara, M. Matelli, M. Gentilucci, *Behav. Brain Res.* **2**, 147 (1981).
- P. B. Johnson, S. Ferraina, L. Bianchi, R. Caminiti, *Cereb. Cortex* **6**, 102 (1996).
- E. G. Jones, J. D. Coulter, S. H. Hendry, *J. Comp. Neurol.* **181**, 291 (1978).
- F. H. Duffy, J. L. Burchfiel, *Science* **172**, 273 (1971).
- H. Sakata, Y. Takaoka, A. Kawarasaki, H. Shibutani, *Brain Res.* **64**, 85 (1973).
- C. L. Colby, J. R. Duhamel, *Neuropsychologia* **29**, 517 (1991).
- M. S. Graziano, M. Botvinick, in *Common Mechanisms in Perception and Action, Attention and Performance XIX* (Oxford Univ. Press, Oxford, 2001), pp. 136–157.
- E. Macaluso, J. Driver, *Adv. Neurol.* **93**, 219 (2003).
- E. Naito, P. E. Roland, H. H. Ehrsson, *Neuron* **36**, 979 (2002).
- C. Kertzman, U. Schwarz, T. A. Zeffiro, M. Hallett, *Exp. Brain Res.* **114**, 170 (1997).
- Y. Burnod et al., *Exp. Brain Res.* **129**, 325 (1999).
- R. A. Andersen, L. H. Snyder, D. C. Bradley, J. Xing, *Annu. Rev. Neurosci.* **20**, 303 (1997).
- H. H. Ehrsson, C. Spence, R. E. Passingham, unpublished data.
- Supported by the Wellcome Trust and by postdoctoral grants from STINT (the Swedish Foundation for International Cooperation in Research and Higher Education) and the Human Frontier Science Program (H.E.E.). We thank R. Deichmann for advice on MRI. For further acknowledgments, see (8).

Supporting Online Material

www.sciencemag.org/cgi/content/full/1097011/DC1

Materials and Methods

SOM Text

Figs. S1 to S4

Tables S1 to S3

References

20 February 2004; accepted 2 June 2004

Published online 1 July 2004;

10.1126/science.1097011

Include this information when citing this paper.

Brood Parasitic Cowbird Nestlings Use Host Young to Procure Resources

Rebecca M. Kilner,^{1*} Joah R. Madden,¹ Mark E. Hauber^{2,3}

Young brood parasites that tolerate the company of host offspring challenge the existing evolutionary view of family life. In theory, all parasitic nestlings should be ruthlessly self-interested and should kill host offspring soon after hatching. Yet many species allow host young to live, even though they are rivals for host resources. Here we show that the tolerance of host nestlings by the parasitic brown-headed cowbird *Molothrus ater* is adaptive. Host young procure the cowbird a higher provisioning rate, so it grows more rapidly. The cowbird's unexpected altruism toward host offspring simply promotes its selfish interests in exploiting host parents.

Parents provisioning young commonly balance the effort they spend on rearing their current brood with the effort they might devote to future offspring (1, 2). Members of the current brood then become rivals for limited parental resources [intra-brood conflict (3, 4)] and must also compete with future offspring to increase the total effort that parents will devote to the current breeding attempt [inter-brood conflict (5)]. In theory, the intensity of both forms of

conflict should increase as offspring relatedness declines, all else being equal (3, 6–9). We used an avian brood parasite to test the importance of relatedness in determining interactions between broodmates.

Obligate avian brood parasites lay their eggs in nests belonging to other species, leaving each of their nestlings to grow up in a family to which it is entirely unrelated (10). The host's nestlings offer formidable competition for resources (11, 12). Nonetheless, in contrast to many cuckoo and honeyguide species, the *Clamator* cuckoos, *Vidua* finches, and parasitic cowbirds tolerate the company of host young in the nest. Nestmate tolerance is unlikely to be explained by kin selection because, although multiple parasitism of individual host nests is common (10), parasite siblings

¹Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK. ²School of Biological Sciences, University of Auckland, PB 92019, Auckland, New Zealand. ³Department of Integrative Biology, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA.

*To whom correspondence should be addressed. E-mail: rmk1002@hermes.cam.ac.uk

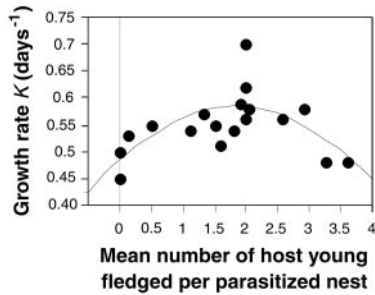


Fig. 1. Relationship between cowbird growth rate and mean number of host young fledged per successful parasitized nest, for cowbirds reared in the nests of 18 different host species. Each data point shows the cowbird's growth rate (K) in one of the 18 host species. Cowbird growth rates were taken from (20). A second-order polynomial regression line is shown. Sources for the number of host young surviving in parasitized nests are given in table S1.

are not typically raised in the same nest (10). Host tolerance by brown-headed cowbird nestlings is especially intriguing because they have been filmed evicting young from the nest (13), yet they apparently refrain from this behavior on most other occasions.

One possibility is that host young bring parasites direct benefits because collectively they evoke a higher level of provisioning than the parasite could ever achieve alone (14–16). We tested this hypothesis with the brown-headed cowbird (44 g), a North American brood parasite that successfully victimizes more than 100 host species (10). Cowbirds reduce host reproductive success by removing eggs, lowering hatching success, and starving young (17, 18). To some degree, therefore, cowbirds (both mothers and young) can manipulate the competitive environment in which young parasites are raised. The extent of offspring mortality varies widely from host to host, but one or more host nestlings commonly survive to fledge with the cowbird (19).

We began by using data from the literature for cowbirds reared by 18 host species (20) to test whether cowbirds could ever profit from the survival of host young (21). We examined the association between the number of host young in the nest and cowbird growth rate, because growth rate is a correlate of post-fledging fitness in other songbirds (22). We found that the relationship could be explained by a quadratic regression curve [$F_{2,17} = 6.32, P = 0.010, R^2 = 0.46$: host young partial $t_{17} = 3.54, P = 0.003$; (host young)² partial $t_{17} = -3.44, P = 0.004$], which peaked at a growth rate corresponding with 1.8 host young (Fig. 1) (21). One interpretation of this result is that the brown-headed cowbird benefits from sharing the nest with host young, and that its optimal number of host companions is approximately two [see also (16)].

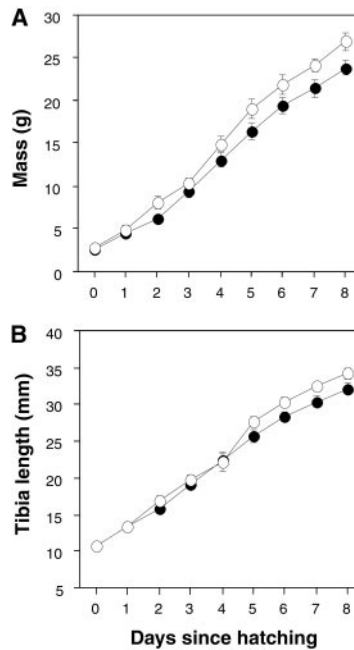


Fig. 2. Change in (A) mass and (B) tibia length with age for cowbirds reared alone ($N = 10$; black circles) or with two phoebe young ($N = 10$; white circles). Means with SE bars are shown.

We tested this interpretation with experiments that focused on the cowbird's interactions with one host, the Eastern phoebe *Sayornis phoebe* (20 g), a migrant flycatcher that typically rears broods of five phoebe young. At our study site in Tompkins County, New York, USA (19, 23), one to three host offspring survived to fledge at 62% of naturally parasitized nests ($N = 29$ broods with one cowbird chick, 1999–2001). In April and May 2003, we monitored 81 phoebe nests during egg-laying and arranged for 20 nests to be parasitized with a single cowbird egg. At 10 of these nests, we removed host eggs on the day the cowbird nestling hatched so that it would be reared alone. At the remaining 10 nests, we removed host eggs and introduced two phoebe nestlings per nest, which had hatched either on same day as the cowbird chick ($N = 8$) or a day later ($N = 2$). Molecular sexing later revealed that we had assigned equal numbers of male and female cowbird nestlings to the two treatments by chance. On hatch day, and every day thereafter for 9 days, we weighed chicks and measured their tibia length, and calculated the instantaneous growth constant K to summarize rates of mass gain and skeletal growth (21).

We found that cowbird nestlings that were accompanied by host young in the nest gained mass at a greater rate (Mann-Whitney U test: $Z = -2.003, P = 0.045$) and showed faster skeletal growth (unpaired $t_{18} = -2.59,$

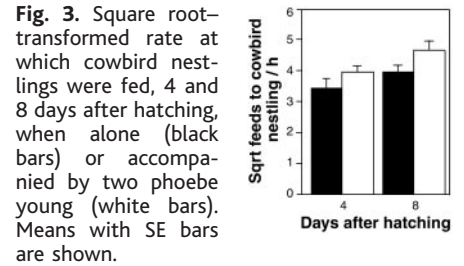


Fig. 3. Square root-transformed rate at which cowbird nestlings were fed, 4 and 8 days after hatching, when alone (black bars) or accompanied by two phoebe young (white bars). Means with SE bars are shown.

$P = 0.019$; Fig. 2) than those reared alone. By day 8, cowbirds reared with host young were, on average, 14% heavier than cowbirds reared alone (unpaired $t_{16} = -2.23, P = 0.041$; Fig. 2A). To determine how the presence of host young benefited cowbird nestlings, we filmed each nest twice, 4 and 8 days after hatching, and scored the hourly provisioning rate to chicks in the nest. Pooling data from both days, we found that parents brought food to nests containing a cowbird and two phoebe nestlings more frequently (mean \pm SEM = 36.4 ± 3.85 feeds/hour) than to nests containing a lone cowbird (14.2 ± 1.62 feeds/hour). Cowbirds took an average of $55.7 \pm 2.9\%$ of feeds in mixed broods, which is a significantly greater share than the 33% expected by chance (Wilcoxon signed rank test, $Z = 3.73, P < 0.001$). As a result, cowbirds reared with host young obtained more food in total than cowbirds reared without competitors [analysis of variance (ANOVA): brood manipulation effect, $F_{1,30} = 5.14, P = 0.031$; Fig. 3]. Older broods were provisioned more frequently (ANOVA: chick age effect, $F_{1,30} = 3.23, P = 0.029$), but the cowbird's share of the food did not change with age (ANOVA: brood manipulation \times chick age interaction, $F_{1,30} = 0.17, P = 0.68$).

Accompanied cowbirds may have experienced a higher provisioning rate because the collective begging behavior of the brood presented a greater stimulus to parents, or because parents were more responsive to the begging behavior of their own young (24). Alternatively, it may have been that the longer periods of brooding experienced by lone cowbirds slowed the rate at which these parasites were fed (ANOVA, brood manipulation effect: $F_{1,30} = 4.92, P = 0.034$) (21). However, the latter explanation seems unlikely because the brooding effort devoted to lone cowbirds was not significantly related to the rate at which they were fed (simple linear regression, time spent brooding versus provisioning rate: $F_{1,16} = 0.07, P = 0.94$), probably because male phoebes continued to feed the cowbird as it was brooded by the female (23).

Our results show that cowbirds exploit host parents to a greater extent by using host young to procure food. Cowbirds capitalize on the increased provisioning that

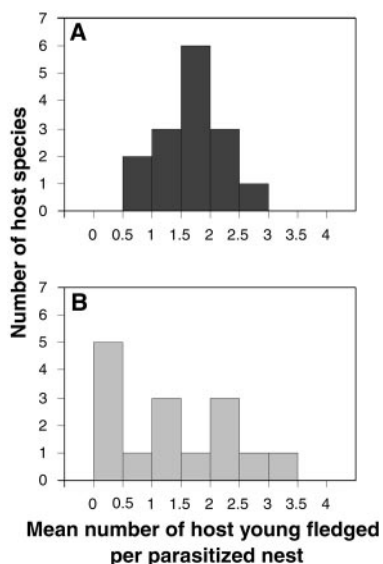


Fig. 4. Frequency distributions of mean numbers of host young fledging from successful nests of (A) hosts within the cowbird's historic range ("old" hosts) and (B) hosts victimized as a result of the cowbird's recent range expansion ("new" or "intermediate" hosts). The data set uses 30 of the species in (37) and their descriptions of the duration of host-cowbird sympatry. The sources of data for the mean host young fledged in parasitized nests of the different host species are given in (27). We calculated the difference between the "ideal" number of host young (= 1.8 from Fig. 1) and the observed numbers of host young for "old" and "new" hosts. The magnitude of difference was much greater for "new" hosts than for "old" hosts (unpaired $t_{28} = 2.94$, $P = 0.007$), even after controlling for phylogenetic effects with pairwise comparisons of closely related "new" and "old" host species (paired $t_4 = 2.79$, $P = 0.049$).

results from additional young in the nest by consistently outcompeting host nestlings to obtain extra parental feedings. Furthermore, there appears to be an optimal number of roughly two host young that are of use to the cowbird (Fig. 1). Larger numbers

of host nestlings may take too much of the additional food collectively solicited by the brood. We note that cowbirds reared in the nests of hosts within the cowbird's historic range are most frequently accompanied by an average of 1.5 to 2 host young (Fig. 4), but further experiments are required to explain this association fully.

Our study shows that there are costs associated with the loss of assistance in soliciting care, as hypothesized previously (14–16). It means that both the benign and virulent behavioral strategies of young brood parasites toward host nestmates can now be viewed as adaptive, each the result of a different balance between the costs of sharing resources with rivals and the benefits of retaining assistance in soliciting care. Our experiments also have implications beyond host-parasite interactions, suggesting that selection acts on avian broods at two levels (25, 26): through the competitive success of individual offspring, and through the parental provisioning rates evoked by the brood collectively. If offspring must restrain their selfishness in intrabrood conflict to attract a more frequent provisioning rate, then they cannot simultaneously "win" intrabrood conflict and interbrood conflict (27, 28). The extent of parent-offspring conflict seen in avian families may therefore depend on the interplay between intrabrood conflict and interbrood conflict (29, 30).

References and Notes

1. R. L. Trivers, in *Sexual Selection and the Descent of Man 1871–1971*, B. Campbell, Ed. (Aldine, Chicago, 1972), pp. 136–179.
2. L. Gustafsson, W. J. Sutherland, *Nature* **335**, 813 (1988).
3. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
4. M. Macnair, G. A. Parker, *Anim. Behav.* **27**, 1202 (1979).
5. R. L. Trivers, *Am. Zool.* **14**, 249 (1974).
6. G. A. Parker, M. Macnair, *Anim. Behav.* **27**, 1210 (1979).
7. J. Maynard Smith, *Anim. Behav.* **42**, 1034 (1991).
8. H. C. J. Godfray, *Nature* **376**, 133 (1995).
9. R. A. Johnstone, *Proc. Natl. Acad. Sci. U.S.A.* **96**, 12644 (1999).

10. N. B. Davies, *Cuckoos, Cowbirds and Other Cheats* (Poyser, London, 2000).
11. D. C. Dearborn, *Behav. Ecol. Sociobiol.* **43**, 259 (1998).
12. G. Lichtenstein, S. G. Sealy, *Proc. R. Soc. London Ser. B* **265**, 249 (1998).
13. D. C. Dearborn, *Condor* **98**, 645 (1996).
14. G. Lichtenstein, thesis, University of Cambridge (1997).
15. A. Lotem, *Trends Ecol. Evol.* **13**, 342 (1998).
16. R. M. Kilner, *Anim. Behav.* **66**, 569 (2003).
17. S. I. Rothstein, *Condor* **77**, 250 (1975).
18. R. M. May, S. K. Robinson, *Am. Nat.* **126**, 475 (1985).
19. M. E. Hauber, *Behav. Ecol.* **14**, 227 (2003).
20. A. M. Kilpatrick, *Can. J. Zool.* **80**, 145 (2002).
21. See supporting data at Science Online.
22. S. Gebhardt-Henrich, H. Richner, in *Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum*, J. M. Starck, R. E. Ricklefs, Eds. (Oxford Univ. Press, New York, 1998), pp. 324–339.
23. M. E. Hauber, K. Montenegro, *Etolgia* **10**, 1 (2002).
24. R. B. Payne, J. L. Woods, L. L. Payne, *Anim. Behav.* **62**, 473 (2001).
25. H. K. Reeve, L. Keller, in *Levels of Selection in Evolution*, L. Keller, Ed. (Princeton Univ. Press, Princeton, NJ, 1999), pp. 3–14.
26. D. Sloan Wilson, A. B. Clark, in *The Evolution of Begging: Competition, Cooperation and Communication*, J. Wright, M. L. Leonard, Eds. (Kluwer Academic, Dordrecht, Netherlands, 2002), pp. 43–64.
27. G. A. Parker, D. W. Mock, T. C. Lamey, *Am. Nat.* **133**, 846 (1989).
28. L. S. Forbes, *Am. Nat.* **142**, 82 (1993).
29. D. Haig, *J. Evol. Biol.* **9**, 357 (1996).
30. M. A. Rodríguez-Gironés, *Proc. R. Soc. London Ser. B* **266**, 2399 (1999).
31. S. A. Hosoi, S. I. Rothstein, *Anim. Behav.* **59**, 823 (2000).
32. R.M.K. is supported by a Royal Society University Research Fellowship. J.R.M. is a postdoctoral research assistant to N. B. Davies (funded by the UK Natural Environment Research Council), and M.E.H. holds a Miller Research Fellowship. We thank C. Wilson, E. and C. Cramer, and the many residents of Tompkins County who kindly allowed us access to nests on their property; D. W. Winkler and his lab for logistical support; N. Flanders for assistance in the field; and M. de L. Brooke, N. B. Davies, E. H. DuVal, C. A. Hinde, S. Hunt, E. A. Lacey, N. E. Langmore, K. M. Pilz, T. D. Price, A. F. Russell, J. G. Schuetz, P. W. Sherman, three anonymous referees, and many others for discussion or comments on the manuscript.

Supporting Online Material

www.sciencemag.org/cgi/content/full/305/5685/877/DC1

Materials and Methods

Table S1

References

30 March 2004; accepted 30 June 2004

Turn a new
page to...

www.sciencemag.org/books

Science
Books et al.
HOME PAGE

- ▶ the latest book reviews
- ▶ extensive review archive
- ▶ topical books received lists
- ▶ buy books online