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Viewpoint

Wild number sense in brood parasitic Brown-headed Cowbirds

JASON LOW,[1*] KEVIN C. BURNS[2] & MARK E. HAUBER[3]
[1]*School of Psychology, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand*
[2]*School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand*
[3]*Department of Psychology, Hunter College, City University of New York, 695 Park Avenue, New York, NY 10065, USA*

Brood parasitic birds provide an innovative model system for studying number sense in wild animals because they need to remember the spatial location of potential nests to lay their eggs and temporal changes in the number of eggs they contain. Brown-headed Cowbirds *Molothrus ater* are extreme host generalists that parasitize over 200 bird species differing greatly in nest location, body mass, clutch sizes, and incubation period (Friedmann *et al.* 1977). Cowbirds lay one egg/day just before sunrise and utilize different places in the landscape for nest finding in the mornings and feeding in the afternoons (Rothstein *et al.* 1984). Clayton *et al.* (2001) suggested that Cowbirds would need to remember the what, where and when of nest-searching events on any given day's exploration to facilitate the laying of physiologically committed eggs the following sunrise and on the days beyond (see also Shaw & Hauber 2009).

As obligate brood parasites, the fitness of Cowbirds critically relies on their ability to synchronize nest parasitism with host incubation readiness. In addition, hatchling Cowbirds compete with host nestmates for parental provisions (Tonra *et al.* 2008), unlike some parasitic cuckoo or honeyeater chicks, which evict or slaughter host-eggs and chicks (Davies 2000). The clutch sizes of passerine hosts range from two to eight eggs and incubation times range from 11 to 16 days (Friedmann *et al.* 1977). Therefore, some information about a nest's readiness for incubation could be gleaned from the daily increase in the number of eggs in a nest until incubation begins at the penultimate egg and clutch size stabilizes. Consequently, the ability to remember the number of host-eggs present in nests and changes in host-egg number between past and present visits is likely to be selectively advantageous. Here we speculate on the flexibility and mechanism of Cowbirds' spontaneous number representation by discussing a new landmark study by White *et al.* (in press).

White *et al.* (in press) report that Cowbirds make egg-laying decisions based on the changes in egg numbers in the nests of potential hosts, providing exciting new evidence that their reproductive decisions are modulated by a representation of host-egg number. In one experiment, White *et al.* observed that Cowbirds spent more time investigating a three-egg nest than a one-egg nest. Then nests were screened off, allowing the birds to see them only from afar. The experimenters then added eggs into the two artificial nests at different rates. To the initial three-egg nest, they added one egg daily for three days, simulating a host that was still laying eggs. To the initial one-egg nest, only two eggs were added over the course of the next 3 days. Consequently, this nest contained a total number of eggs that did not match the number of days elapsed, simulating the nest of a host that has begun incubation. When the screen was removed, Cowbirds spent more time investigating the nest most likely ready for incubation, that is, the six-egg nest. Such decisions could have been based on sensory cues (e.g. the greater visual and tactile area of six eggs) rather than number *per se* (e.g. Hauber & Sherman 2001). So, in another experiment, White *et al.* presented Cowbirds with three nests whose contents changed daily or did not change numerically over time (set-up in Fig. 1 Panel I).

On Day-1, Cowbirds parasitized nests with the most host-eggs (i.e. nest C1 with three eggs). On Day-2, Cowbirds parasitized nests that changed in egg-number from the day before (i.e. nests A2 and B2). The critical test was egg-laying behaviour on Day-3, when all nests were identical. Cowbirds preferentially parasitized nests that changed in egg-number in accordance with the number of days that had elapsed from their initial visit (i.e. nest A3). Therefore, Cowbirds appeared to remember changes in egg-number between visits and spent longer periods investigating nests with the *correct* accumulated number of eggs in relation to elapsed days (i.e. nest parasitism followed solid arrows in Fig. 1, Panel I).

Recently, Hunt *et al.* (2008) investigated the number sense of a food-hoarding songbird (the New Zealand Robin *Petroica australis*) wherein Robins watched an experimenter place mealworms in an artificial cache site with a hidden trap door. Robins searched for longer when the quantity of hidden food stock *violated* addition rules when some were hidden behind the trap door (e.g. 1 worm + 1 worm = 1 worm). One implication of White *et al.*'s (in press) work is that Cowbirds may recognize host readiness for clutch completion and incubation *vis-à-vis* changes in egg number, but whether they also symbolically operate on host nests by adding

*Corresponding author.
Email: Jason.Low@vuw.ac.nz.

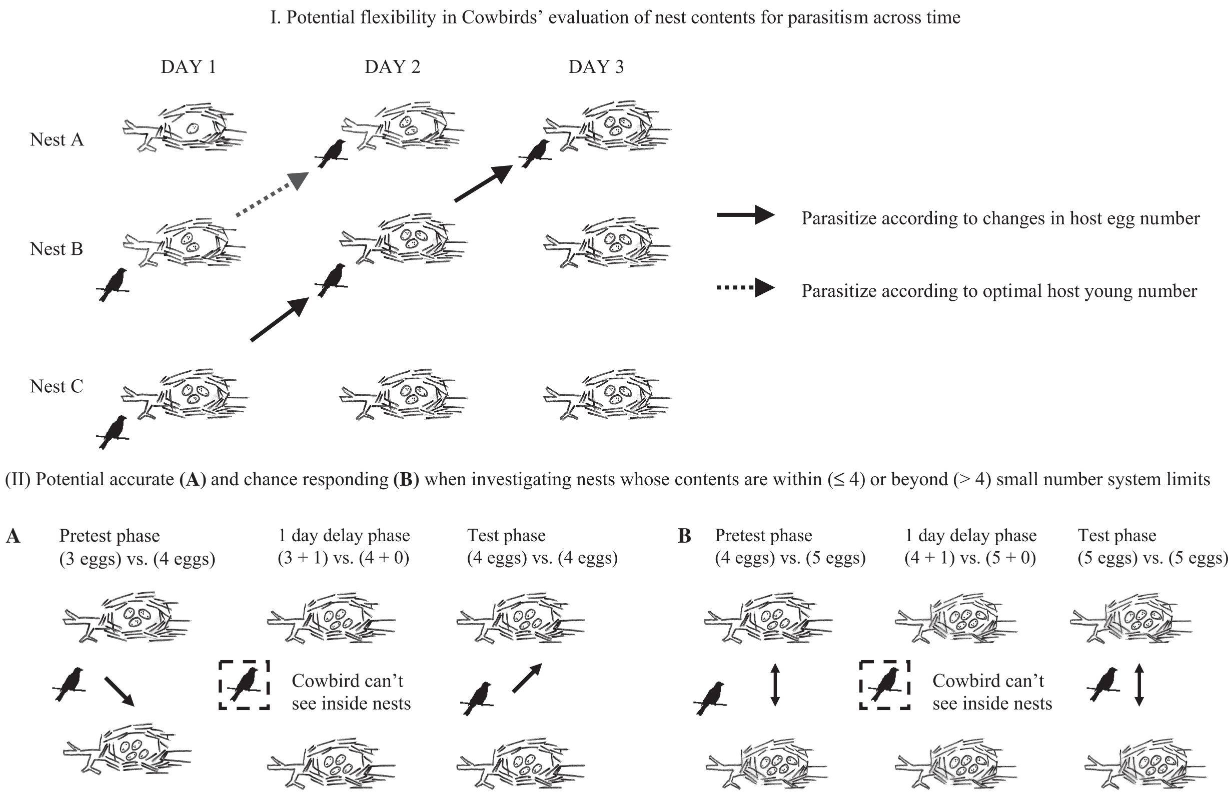

Figure 1. Potential flexibility in and exact limits to Cowbirds' spontaneous numerical representations. I. Potential flexibility in Cowbirds' evaluation of nest contents for parasitism across time. II. Potential accurate (A) and chance responding (B) when investigating nests whose contents are within (≤ 4) or beyond (> 4) small number system limits.

up host-eggs to yield numerical representations of the resulting nests remains unknown. How might Cowbirds respond when the number of eggs found is *greater* than the number of days elapsed? Would Cowbirds spend more time investigating nests with 'too many' eggs? It is worth stressing that it is not yet clear why birds would need to develop numerical skills in the first place. A prominent exception is a study on American Coots *Fulica americana* which found that potential hosts experiencing intraspecific brood parasitism adjusted their clutch sizes by counting the number of eggs in the nest that are perceived as their own (Lyon 2003). White *et al.*'s study of brood-parasitic Cowbirds, in addition to Hunt *et al.*'s work on food-caching Robins, contributes to new evidence of wild birds developing and adaptively using sophisticated number sense relevant to their own ecology.

The implications of White *et al.*'s (in press) research are relevant for brood parasite biology, as female Cowbirds face a conundrum. They benefit when their chick is competitively superior to host chicks (i.e. larger, hatches earlier: Kilner 2003), but they also benefit when some of the host chicks survive alongside the parasitic chick to help facilitate parental provisioning (Kilner *et al.* 2004). Consequently, Cowbirds may also seek to parasitize nests with an optimal number of nest-mates for their young. Around two host-young optimizes extra foster-parent feeding for the Cowbird fledgling (Kilner 2003) (i.e. nest-parasitism may also follow the dashed arrow shown in Fig. 1, Panel I). In other situations, Cowbirds may keep track of conspecific eggs. For example, whilst adult females avoid nests containing Cowbird eggs, juveniles seem to prefer those parasitized nests (as shown by prior experimentation in White *et al.* 2007). For a female Cowbird who is a first-time breeder, the presence of another Cowbird egg may indicate the suitability of that host nest for parasitism. However, this strategy may only be feasible up to when there are two or three Cowbird eggs per nest – it is costly for Cowbirds to compete with other parasite hatchlings (Trine 2000). Overall, there may be additional fine-tuned abilities of female Cowbirds to assess and prefer clutch contents which predict optimal survival for their parasitic young. Advanced numerical bookkeeping such as this may have important implications for Cowbird social structure and host–parasite arms races in general (Davies 2000).

White *et al.* (in press) found that Cowbirds parasitized nests with the larger egg number in comparisons involving 1 vs. 2, 2 vs. 3 and 1 vs. 3 eggs. Could Cowbirds' attention to egg number be partly supported by the small precise number system? This system's processing signature is an upper limit in set discriminations at around three to four objects (Feigenson *et al.* 2004). However, it is not yet known whether this set-size effect applies to Cowbirds. For example, will Cowbirds make accurate numerical decisions when changes to egg numbers are made in a 3 vs. 4 contrast, but not when changes are made in a 4 vs. 5 contrast (Fig. 1, Panel II)? Dovetailing experimental with ecological research may reveal whether a small set-size limit overlaps with how Cowbirds optimally grow up with a small number of host nest-mates and how female Cowbirds avoid parasitizing nests with greater than three to four Cowbird or host eggs (Trine 2000).

White *et al.*'s (in press) new work into the Cowbird model system excitingly suggests that brood parasites can count host chicks before they hatch. However, the system still remains a cognitive black-box; ornithological research might help us clarify the contextual flexibility and core mechanism underpinning Cowbirds' number sense. Nonetheless, together with high profile discoveries that female Cowbirds monitor host nests and retaliate against rejecters (Hoover & Robinson 2007), and extensive work on the complex neuro-anatomical basis of spatial memory systems in nest-searching brood parasites (e.g. Reboreda *et al.* 1996), Cowbirds now appear to be an excellent behaviourally testable model system to investigate avian cognition. Further research into the Cowbird model system may illuminate why some birds evolve to become 'math-brained' instead of 'bird-brained'.

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