1 Smarter through group living: A response to Smulders

2 Authors: Benjamin J. Ashton^{1*}, Amanda R. Ridley¹, Alex Thornton²

3 Affiliations:

- 4 ¹Centre for Evolutionary Biology, School of Biological Sciences, University of Western Australia, 35
- 5 Stirling Highway, Crawley 6009, Australia.
- ²Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Treliever Road, Penryn
 TR10 9FE, UK
- 8 *Correspondence to: benjamin.ashton@research.uwa.edu.au

9 Abstract

10 In our recent paper(Ashton, Ridley, Edwards, & Thornton, 2018) we investigated the causes of 11 individual variation in cognitive performance in the Australian magpie *Cracticus tibicen dorsalis*. We 12 presented individuals with a cognitive test battery consisting of four tasks designed to quantify 13 behavioural inhibition, associative learning, reversal learning, and spatial memory. We reported a 14 strong, positive relationship between group size and individual performance in all four tasks of the 15 cognitive test battery(Ashton, Ridley, et al., 2018). Furthermore, females that performed better in 16 the cognitive test battery had greater reproductive success (a greater number of successful clutches 17 per year, fledglings per year, and fledglings surviving to independence per year), compared to 18 females that performed badly (Ashton, Ridley, et al., 2018). An opinion piece by Smulders (2018) 19 raised the interesting notion that these patterns may be underlined by motivational factors. In this 20 commentary we highlight why none of the available data is consistent with this explanation, but 21 instead support the argument that the demands of group living influence cognitive development, 22 with knock-on consequences for fitness.

23 Key words

24 Social intelligence hypothesis, cognitive ecology, Australian magpie

25 In the last few years the field of cognitive ecology has increasingly begun to recognise the 26 importance of adopting an intraspecific approach, focusing on the causes and consequences of 27 individual variation in cognitive performance(Ashton, Thornton, & Ridley, 2018; Boogert, Madden, 28 Morand-Ferron, & Thornton, 2018; Morand-Ferron, Cole, & Quinn, 2015; Thornton & Lukas, 2012). A 29 number of important recent advances have been made in the field, including the identification of 30 links between cognitive performance and group size(Ashton, Ridley, et al., 2018; Langley, Horik, 31 Whiteside, & Madden, 2018), effects of spatial memory on survival (Maille & Schradin, 2016) and 32 evidence for a "general cognitive factor" underpinning performance across a range of tasks in birds 33 (Shaw, Boogert, Clayton, & Burns, 2015). However, determining that observed differences in 34 individual performance result from cognitive differences rather than other factors is extremely 35 challenging (Boogert et al., 2018; Rowe & Healy, 2014; Thornton, Isden, & Madden, 2014), so the 36 results of these studies need to be interpreted with great caution. This is particularly the case where 37 studies are carried out on wild populations of animals, where results are often correlational because 38 experimental manipulations may be logistically challenging, or (in some cases) impossible. In our 39 work on Australian magpies, for instance, experimental manipulations of group size were neither logistically or ethically feasible, so a causal effect of group size on individual cognitive performance 40 41 could not be determined unequivocally. Nevertheless, we took great pains to rule out alternative 42 explanations for the observed relationship.

Smulders (2018) suggests individuals living in larger groups may face greater competition for food,
and therefore have greater motivation to interact with experimental tasks, which may explain the
positive relationship between group size and cognitive performance reported in our study (Ashton,
Ridley, et al., 2018). First, we note that a positive association between group size and food
competition is by no means a universal phenomenon; indeed several studies show that foraging
intake can increase with increasing group size (Blundell, 2002; Courchamp, Rasmussen, &

49 Macdonald, 2002; Sorato, Gullett, Griffith, & Russell, 2012). More specifically, several lines of 50 evidence suggest differences in motivation do not underpin the group size- cognition relationship in 51 Australian magpies. We examined the potential effect of two factors likely to influence food 52 motivation: body mass and foraging efficiency (defined as the mass of food (in grams), caught per 53 foraging minute (Edwards, Mitchell, & Ridley, 2015)). Less efficient foragers (who might be predicted 54 to be hungrier), and individuals in poor condition (potentially indicated by body mass), might be more motivated to engage with the tasks and therefore perform better. Neither of these factors 55 56 predicted cognitive performance (Ashton, Ridley, et al., 2018). Furthermore, additional analyses 57 show there was no relationship between foraging efficiency and group size (Spearman's correlation, 58 $r_s = -0.097$, p = 0.458, n = 61 individuals across 14 groups ranging in size from 3 - 12), suggesting 59 there is no difference in food competition between groups of different sizes. Although food 60 motivation is expected to vary over time in response to prevailing conditions, we found that 61 individual cognitive performance was highly consistent, with individuals showing strong repeatability 62 when tested on different versions of each task (Ashton, Ridley, et al., 2018). We also examined the 63 potential effects of factors that may be direct indicators of food motivation, namely the latency to 64 interact with the task, and time spent interacting with the task ("task attention"). One would expect 65 more food motivated birds to approach the task more quickly and spend more time engaged with 66 the task; if our results were driven by food motivation, we would therefore predict latency to 67 interact with the task and time spent interacting with the task to explain variation in cognitive 68 performance. However, neither of these factors predicted cognitive performance (Ashton, Ridley, et 69 al., 2018). For these reasons, differences in motivation are unlikely to drive the positive relationship 70 between group size and cognitive performance.

Repeated testing of juveniles showed that the relationship between group size and cognitive
performance emerged after 100 days post-fledging (Ashton, Ridley, et al., 2018), consistent with the
idea that the size of the group an individual grows up in has an influence on its cognitive
development (we note that at day 100 it was only possible to quantify performance in behavioural

75 inhibition and spatial memory because fledglings at this age were unable to pass the associative and 76 reversal learning tasks, regardless of their group size (see methods, Ashton, Ridley, et al., 2018)). 77 Smulders (2018) suggests motivation may also explain the emergence of the group size-cognition 78 relationship in juveniles. However, much like the adults, neither body mass (Pearson's correlation, r 79 = 0.291, p = 0.2, n = 21 individuals tested from 11 groups ranging in size from 3-12) nor latency to 80 interact with the task (Spearman's correlation, r = -0.144, p = 0.532, n = 21 individuals tested from 81 11 groups ranging in size from 3-12) correlated with group size in juveniles, suggesting there is no 82 difference in motivation between groups (the correlations reported were for juveniles at 100 days 83 post-fledging, but results were qualitatively the same for all ages). Furthermore, body mass and 84 latency to interact with the tasks did not predict cognitive performance when the group size-85 cognition relationship had emerged at both 200 and 300 days post-fledging (Ashton, Ridley, et al., 86 2018).

87 We found strong positive correlations in individual performance across the four tasks in our test 88 battery. On the basis of these findings, Smulders(2018) suggests we "jump to conclusions about 89 general intelligence" in Australian magpies. While we point out the parallels between our results and the literature on "general intelligence", we deliberately avoid the term when discussing our findings 90 91 and follow Shaw et al. (2015) in using the more neutral term "general cognitive performance". We 92 are also careful to be open about the fact that the underlying causes of correlations between 93 performance on different tasks are not understood (supplementary material: "It is, however, worth 94 noting that the underlying causes of the correlations in performance among tasks are not known. It 95 is, for instance, possible that some performance in all tasks may place similar demands on working 96 memory (e.g. in colour discrimination individuals must not only learn, but remember which colour 97 was rewarded)" Ashton, Ridley, et al., 2018). However, we wholeheartedly agree that expanding the 98 cognitive test battery to include a greater variety of tests covering a wider range of cognitive 99 domains will help elucidate the extent to which Australian magpie cognition is underpinned by 100 domain-general processes (see also Whiten, 2018). The suggestion to test dispersed juveniles is

101 another excellent idea, although contrary to Smulders' argument, non-territorial flocks of juveniles 102 occur only in the Eastern (non-cooperatively breeding) subspecies of Australian magpie, not in the 103 Western subspecies we studied (Johnstone & Storr, 2004). Likewise, further investigation of the 104 relationship between provisioning rate and female cognitive performance is an important future 105 research objective that will help elucidate the causes and consequences of individual variation in 106 cognition in Australian magpies. However, we reiterate there is no evidence to suggest females in 107 larger groups are more food-motivated, indicating that if a relationship between female cognitive 108 performance and female provisioning rate did emerge, it is likely to be underpinned by cognitive 109 processes.

In summary, as Smulders suggests, the results of observational studies are often open to alternative
 explanations, but the evidence accumulated from our research provides compelling evidence that, in
 Australian magpies at least, living in large groups has positive cognitive consequences.

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