Developmental and familial predictors of adult cognitive traits in the European starling

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In birds, there is evidence that adult cognitive traits can both run in families and be affected by early developmental influences. However, different studies use different cognitive tasks, which may not be measuring the same traits, and also focus on different developmental factors. We report results from a study in which we administered multiple cognitive tasks (autoshaping, discrimination learning, reversal learning, progressive ratio schedule, extinction learning and impulsivity) to a cohort of 34 European starlings, *Sturnus vulgaris*, for which several early developmental measures were available. The cohort consisted of siblings raised either apart or together, whose position in the size hierarchy of the rearing brood had been experimentally manipulated. We examined how the different cognitive measures co-varied, the extent to which they ran in families, and which of the developmental factors predicted which of the cognitive outcomes. We found that discrimination and reversal learning speeds were positively correlated, as were breakpoint on the progressive ratio schedule and resistance to extinction. Otherwise, the cognitive measures were uncorrelated, suggesting that they reflected different underlying traits. All traits except discrimination and reversal learning speed ran in families to a substantial extent. Using a model selection approach, we found evidence that natal brood size and developmental telomere attrition (the extent to which the birds' erythrocyte telomeres shortened in early life, an integrative measure of developmental stress) were related to several adult cognitive measures. Results are discussed with respect to the best way of measuring avian cognitive abilities, and the utility of developmental telomere attrition as a predictor of adult outcomes.

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Evidence from several different taxa, including humans, suggests that conditions experienced during early development can influence cognitive traits in adulthood (Avital, Ram, Maayan, Weizman, & Richter-Levin, 2006; Frankenhuis & de Weerth, 2013; Nowicki, Searcy, & Peters, 2002; Oomen et al., 2010; Sampson, Sharkey, & Raudenbush, 2008). In some cases, developmental adversity is associated with impaired adult cognitive abilities. For example, three studies have found that patterns of early growth are related to learning speed in zebra finches, *Taeniopygia guttata* (Bonaparte, Riffle-Yokoi, & Burley, 2011; Brust, Krüger, Naguib, & Krause, 2014; Fisher, Nager, & Monaghan, 2006).

In other cases, adverse developmental conditions may induce adaptive shifts, rather than impairments, in cognition (Frankenhuis & de Weerth, 2013; Oomen et al., 2010). In a recent study in European starlings, *Sturnus vulgaris* (Bateson, Brilot, Gillespie, Monaghan, & Nettle, 2015), we found that birds that had experienced more developmental telomere attrition (an integrative measure of developmental stress) had a stronger preference for immediate over delayed rewards as adults. We argued that the cognitive performance of the birds that had experienced poor early conditions was not worse, but simply reflected different priorities. This was borne out by the fact that in these studies there was no relationship between developmental telomere attrition and measures of associative learning speed that were incidentally generated during training. However, the possibility that the effects we observed indicated subtly reduced cognitive ability cannot be excluded.

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While there has been a recent burgeoning of interest in measuring individual differences in cognition in birds (e.g. Boogert, Giraldeau, & Lefebvre, 2008; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Morand-Ferron, Hinks, & Quinn, 2012; Keagy, Savard, & Borgia, 2009), different studies use different cognitive tasks. Thus, it is hard to be sure exactly which aspect of cognition is being captured in each study, especially since some tasks may reflect boldness, neophobia or food motivation more than cognitive ability (Rowe & Healy, 2014; Templeton, Laland, & Boogert, 2014). Where studies have administered multiple tasks to the same individuals, they have mostly found intercorrelations between tasks to be weak or absent, suggesting that multiple independent capacities are being tested (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; Isden, Panayi, Dingle, & Madden, 2013; Keagy, Savard, & Borgia, 2011; Keagy et al., 2009). A notable exception is the positive correlation between trials to acquire a discrimination and trials to acquire its reversal observed in a recent study of song sparrows, *Melospiza melodia* (Boogert et al., 2011). The relationships of the many other commonly used cognitive tasks to learning speed as measured using discrimination and reversal learning are not well established.

We had access to a cohort of captive European starlings whose position in the within-brood size hierarchy had been experimentally manipulated, and whose developmental histories were very well characterized (Nettle et al., 2015). Quartets of chicks had been taken from their natal nests soon after hatching, and cross-fostered, two to a nest where they were slightly larger than the other chicks (advantaged treatment), and the other two to a nest where they were slightly smaller (disadvantaged treatment). The quartets were likely to have consisted of genetic siblings, since intraspecific brood parasitism affects only a minority of nests in the European starling (Pinxten, Eens, & Verheyen, 1991), and no nests were used where the clutch increased by more than one egg per day or the eggs obviously varied in colour. At posthatching day 12, the chicks were brought into captivity and kept in uniform conditions to adulthood. As we have reported previously, the developmental treatment had no effect on their growth curves, but the disadvantaged birds showed greater telomere attrition in early life than their advantaged siblings (Nettle et al., 2015).

The present paper reports the results of experiments conducted when the birds were between 5 and 13 months old, in which we measured, under standardized conditions, performance on a battery of cognitive tasks (see below for description). Our main aims in doing so were the following. First, we sought to investigate the extent to which performance on different tasks covaried; in particular, we were interested in whether discrimination and reversal learning speed were positively correlated, and which other tasks, if any, would also correlate with discrimination and reversal learning speed. Second, we sought to investigate which, if any, of the different measures of early developmental conditions was best at predicting adult cognitive performance. Finally, our design provided an opportunity to examine the extent of natal family influences on cognitive traits, as well as the impact of rearing nest. We found modest familial effects on impulsivity in our previous study (Bateson et al., 2015). By contrast, Bonaparte et al. (2011) found that familial effects on speed to acquire a conditioned discrimination in their zebra finches were trivial. This may suggest that different cognitive measures show different degrees of familial patterning.

Our battery of tasks included autoshaping, discrimination learning, reversal learning, progressive ratio schedule, extinction learning and an impulsivity measure. Autoshaping (Brown & Jenkins, 1968) exploits Pavlovian conditioning. A novel stimulus is repeatedly paired with the delivery of a food reward. The performance measure is the number of trials required before the subject begins to direct an appetitive response at the stimulus. Speed of autoshaping is conventionally interpreted as a measure of reinforcement learning (Markou et al., 2013). However, Feenders and Bateson (2013) concluded that individual differences in speed of autoshaping in starlings may primarily reflect individual differences in neophobia, rather than learning ability.

Discrimination learning involves pairing two arbitrary stimuli such as colours with different reward values (in some versions of the task, one stimulus is rewarded while the other is not; in ours, one was rewarded immediately and the other only after a delay, reducing its value to the starlings). The measure of learning speed is the number of trials required to acquire a preference. Discrimination learning is a relatively pure measure of associative learning ability, since neophobia or boldness can be eliminated as sources of variation. Reversal learning involves reversing the contingencies of the two stimuli once a discrimination has been acquired; the measure is the number of trials required until the subject reverses its previous preference.

In a progressive ratio schedule (Hodos, 1961), the number of instrumental responses required to release a reward is progressively increased. The measure is the breakpoint, the point at which the subject ceases responding. Progressive ratio schedule breakpoint is generally taken as a measure of incentive motivation rather than cognitive ability (Hodos, 1961; Kirkpatrick, Marshall, Smith, Koci, & Park, 2014; Markou et al., 2013); that is, the more motivated by the reward the subject is, the higher the breakpoint will be.

Extinction learning reflects how rapidly an individual ceases to respond to a stimulus that has previously been rewarded but no longer is. Delayed extinction in individuals that have experienced early life adversity has been observed in rodents and nonhuman primates, in which it has been interpreted as resulting from a maladaptive deficit in behavioural inhibition (Beauchamp & Gluck, 1988; Jones, Marsden, & Robbins, 1991).

Finally, we measured impulsivity using an adjusting-delay procedure (Mazur & Biondi, 2009), similar to our previous study (Bateson et al., 2015). Here, impulsivity is conceptualized as the extent to which a reward is devalued by having to wait additional time to receive it. Birds are trained that one stimulus produces a small reward after a short fixed delay, while another stimulus produces a large reward after a long adjustable delay. The length of the adjustable delay is titrated to estimate the point at which the individual is indifferent between the two options. An individual whose indifference point is at a relatively short adjustable delay discounts delay to reward more steeply, and hence is more impulsive, than an individual whose indifference point is at a longer adjustable delay.

Our measures of early life conditions included, in addition to developmental treatment, natal brood size, early growth rate and telomere length change from day 3 to day 12. Natal brood size is likely to reflect the quality or current condition of the genetic mother, with higher-quality or better-condition females laying larger clutches (Christians, Evanson, Aiken, & Aiken, 2001). Early growth rate was a key factor in previous studies of developmental effects on cognition in zebra finches (Bonaparte et al., 2011; Brust et al., 2014; Fisher et al., 2006). Telomere attrition during development is emerging as a useful integrative marker of developmental stress exposure in birds (Boonekamp, Mulder, Salomons, Dijkstra, & Verhulst, 2014; Herborn et al., 2014; Nettle, Monaghan, Boner, Gillespie, & Bateson, 2013), and it was a key predictor of adult cognition in a previous study (Bateson et al., 2015). We also considered adult body condition (defined as weight for skeletal size at time of completing the tasks) as a predictor of the cognitive variables. While not directly a developmental measure, adult body condition is a useful indicator of current state.