



Wild jackdaws' reproductive success and their offspring's stress hormones are connected to provisioning rate and brood size, not to parental neophobia



Alison L. Greggor^{a,b,*}, Karen A. Spencer^c, Nicola S. Clayton^a, Alex Thornton^{d,*}

^a Department of Psychology, University of Cambridge, UK

^b Department of Biological Sciences, Dartmouth College, USA

^c School of Psychology and Neuroscience, University of St. Andrews, UK

^d Department of Biosciences, University of Exeter, Penryn, UK

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ABSTRACT

Many species show individual variation in neophobia and stress hormones, but the causes and consequences of this variation in the wild are unclear. Variation in neophobia levels could affect the number of offspring animals produce, and more subtly influence the rearing environment and offspring development. Nutritional deficits during development can elevate levels of stress hormones that trigger long-term effects on learning, memory, and survival. Therefore measuring offspring stress hormone levels, such as corticosterone (CORT), helps determine if parental neophobia influences the condition and developmental trajectory of young. As a highly neophobic species, jackdaws (*Corvus monedula*) are excellent for exploring the potential effects of parental neophobia on developing offspring. We investigated if neophobic responses, alongside known drivers of fitness, influence nest success and offspring hormone responses in wild breeding jackdaws. Despite its consistency across the breeding season, and suggestions in the literature that it should have importance for reproductive fitness, parental neophobia did not predict nest success, provisioning rates or offspring hormone levels. Instead, sibling competition and poor parental care contributed to natural variation in stress responses. Parents with lower provisioning rates fledged fewer chicks, chicks from larger broods had elevated baseline CORT levels, and chicks with later hatching dates showed higher stress-induced CORT levels. Since CORT levels may influence the expression of adult neophobia, variation in juvenile stress responses could explain the development and maintenance of neophobic variation within the adult population.

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1. Introduction

Neophobia, or the fear of novelty, allows animals to avoid unknown danger, but may also prevent the exploitation of new resources (Greenberg and Mettke-Hofmann, 2001). Individuals who express elevated neophobia may be more likely to survive when predation pressure is high (Ferrari et al., 2015), but they may be at a disadvantage when gathering resources in variable environments, since high neophobia can inhibit behavioral innovation (Benson-Amram and Holekamp, 2012; Greenberg, 2003).

* Corresponding authors at: Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA (A.L. Greggor), Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Treliever Road, Penryn TR10 9FE, UK (A. Thornton).

E-mail addresses: alg61@cam.ac.uk, alisongreggor@gmail.com (A.L. Greggor), alex.thornton@exeter.ac.uk (A. Thornton).

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Although many species are thought to show consistent individual variation in neophobia (Réale et al., 2007), the consequences of this variation in the wild are poorly understood. Behaviors such as neophobia that can be classified as responses to change or uncertainty in the environment, and are consistent at least within seasons, are proposed to have important consequences for individual fitness (Dall et al., 2004). Meta-analyses reveal that less fearful, or “bolder” individuals typically have higher reproductive success (Smith and Blumstein, 2008). However, the majority of evidence for connections between object neophobia and fitness come from studies in which behavioral measures and/or subsequent reproductive success were assessed in captivity (Bremner-Harrison et al., 2004; Janczak et al., 2003; Korhonen et al., 2002; Korhonen and Niemela, 1996; Korhonen et al., 2001). To our knowledge, only one study has found correlations between neophobia and reproductive output in the wild, reporting that neophobic great tits (*Parus major*) had higher occurrences of nest failure

than their less fearful conspecifics (Vrublevska et al., 2015). Direct measures of the impact of neophobia in the wild are rare (although see Schuett et al., 2012). Moreover, even if parental neophobia levels do not impact the gross number of offspring produced, they could have more subtle influences on the rearing environment and the later development of offspring if they prevent the parent from providing adequate or predictable food sources. However, connections between neophobia, foraging ability, and their impact on offspring quality have yet to be tested.

If neophobia levels affect parents' ability to forage for their young, then parental neophobia would be expected to predict measures that indicate developmental stress and offspring quality. Although stress can be caused by numerous factors, such as food deprivation (Pravosudov and Kitaysky, 2006), disrupted maternal care (Banerjee et al., 2012), and acute stressful events (Jacobson-Pick and Richter-Levin, 2010), elevated stress hormones are a common mechanism by which stress impacts a growing organism. One stress hormone, corticosterone (CORT), naturally circulates at a baseline level in the blood to regulate physiological processes such as animals' circadian rhythm. CORT levels also increase dramatically after a stressful event to prime animals for a "fight or flight" response (Romero, 2004; Sapolsky et al., 2000). Therefore, elevated levels of baseline CORT may serve as a marker of ongoing or developmental stress, and exaggerated levels of CORT during stressful events can indicate the magnitude of an individual's fear response (Romero, 2004). Together, the long-term combination of routine CORT release and release during acute stressors determines an individual's allostatic load, i.e. the wear and tear from cumulative stress. A high allostatic load increases the potential for hormone dysregulation (Romero et al., 2009), and may affect their ability to respond to environmental changes (Wingfield, 2013).

Although short-term increases in CORT can help an individual survive a life threatening event, experiencing chronically elevated levels of CORT during development can have long-term effects ranging from impairments in brain structure (Welberg and Seckl, 2001), to reductions in life expectancy (Monaghan et al., 2012), and implications for immune function (Kriengwatana et al., 2013). Long term stress can also decrease the sensitivity of glucocorticoid receptors present in the brain (Banerjee et al., 2012; Hodgson et al., 2007) which potentially modifies the negative feedback loops of stress hormone expression (Romero, 2004; Zimmer et al., 2013). Therefore responses to stress and levels of circulating CORT are often considered stable traits (Evans et al., 2006; Jenkins et al., 2014; Kralj-Fišer et al., 2007; although see Ouyang et al., 2011), and have been suggested to drive individual differences in avian temperament or personality (Baugh et al., 2012; Cockrem, 2007; Moretz et al., 2007). Although many species show individual and population level variation in stress hormone expression (e.g. Cockrem and Silverin, 2002; Grunst et al., 2014; Liebl and Martin, 2012) that can be heritable (Evans et al., 2006), the factors driving this variation differ depending on the species (e.g. food deprivation in western scrub jays, *Aphelocoma californica* Pravosudov and Kitaysky, 2006; sibling competition in barn swallows, *Hirundo rustica* Saino et al., 2003). Therefore the drivers of stress hormone variation are not well understood, despite their potentially far-reaching consequences for development and behavior.

One species that could help disentangle the relationship between neophobia, fitness and offspring rearing environment is the jackdaw (*Corvus monedula*). Like other members of the corvid family, jackdaws are known for having high levels of neophobia in comparison to other species (Greenberg and Mettke-Hofmann, 2001; Greggor et al., 2016a). Individual variation in neophobia and other forms of wariness have been documented in jackdaws (Greggor et al., 2016c; Schuett et al., 2012), but the consequences of their comparatively high neophobia are still unclear. Although a previous study on jackdaws found no relationship between a

single object neophobia measure and the number of chicks produced in one season (Schuett et al., 2012), it is unclear if the neophobia measure was repeatable within the season. Also it is unclear whether or not neophobia would have correlated with nest success had feeding rate—the principal determinant of jackdaw reproductive success (Henderson and Hart, 1993)—been accounted for. Since feeding rate has also been implicated in influencing connections between fitness and responses to novelty in other contexts (e.g. towards a novel environment, at least in females; Mutzel et al., 2013) it could be crucial for determining the origin of neophobia-related fitness effects in jackdaws. Finally, even if parents' neophobia does not influence the net number of chicks they produce per season, it could still broadly impact the quality of the rearing environment and the subsequent physiological stress responses of their offspring. Such influences are critical to determining the potential costs and benefits of neophobic behavior because the effects of developmental impairment could occur after chicks fledge.

We examined the connections between parental neophobia levels, provisioning rates, and breeding success (i.e. fledgling number and quality) in wild breeding jackdaws. We then looked at a subset of nests to assess whether these factors influenced chicks' baseline and stress-induced CORT expression, when other potential influences on CORT such as brood size were considered (Saino et al., 2003). We predicted, similar to what Schuett et al. (2012) reported, that parents' neophobia would not correlate with fledgling number. Instead neophobic variation could influence offspring in other, less direct ways by reducing provisioning rates to an extent that impacts fledgling chicks' body condition or alters baseline circulating CORT and juveniles' propensity to mount a stress-induced hormone response. Therefore even if parents' neophobia does not directly impact chicks' survival in the nest, it could have other long-term impacts on offspring development that would explain selection for or against neophobic behavior.

2. Methods

2.1. Study sites

The study site was situated in forested areas surrounding Madingley Village, Cambridgeshire, UK. Nest boxes were erected on private University of Cambridge land that remains largely undisturbed. During the breeding season of 2013 we tested 68 jackdaw nest boxes on neophobia, and measured CORT levels in 58 chicks from 34 of these boxes. Boxes were clustered into 14 colonies within the study site. Boxes were placed on trees 3–4 m off the ground, such that chicks could be accessed via a large extendable ladder.

The study site was monitored throughout the breeding season. Since jackdaws only have one brood per season, even if their nest fails (Röell, 1978), our monitoring captured the reproductive success of each pair for that year. Laying and hatch dates were determined by daily nest checks. Since jackdaw nests hatch asynchronously, we checked nests daily until all eggs hatched or until several days had lapsed with no new chicks emerging. After all viable eggs hatched, boxes were monitored at least three times a week. Daily checks resumed again at day 28 as the fledging period approached (day 32–34), to provide information on nestling mortality and nest failure. Chicks that died due to starvation could be easily identified because jackdaw parents are unable to remove them from the box once they reach about 10 days of age. We deemed the nest to have fledged once all chicks vacated the box. All nest disturbances were conducted under a Natural England License (20130067 to A.L.G.), blood sampling under Home Office permits (PIL 70/24971 to A.L.G, PPL to A.T. 80/2371) and ringing

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