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# Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position

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Neophobia, or the fear of novelty, may offer benefits to animals by limiting their exposure to unknown danger, but can also impose costs by preventing the exploration of potential resources. The costs and benefits of neophobia may vary throughout the year if predation pressure, resource distribution or conspecific competition changes seasonally. Despite such variation, neophobia levels are often assumed to be temporally and individually stable. Whether or not neophobia expression changes seasonally and fluctuates equally for all individuals is crucial to understanding the drivers, consequences and plasticity of novelty avoidance. We investigated seasonal differences and individual consistency in the motivation and novelty responses of a captive group of rooks, *Corvus frugilegus*, a seasonally breeding, colonial species of corvid that is known for being neophobic. We tested the group around novel objects and novel people to determine whether responses generalized across novelty types, and considered whether differences in dominance could influence the social risk of approaching unknown stimuli. We found that the group's level of object neophobia was stable year-round, but individuals were not consistent between seasons, despite being consistent within seasons. In contrast, the group's avoidance of novel people decreased during the breeding season, and individuals were consistent year-round. Additionally, although subordinate birds were more likely to challenge dominants during the breeding season, this social risk taking did not translate to greater novelty approach. Since seasonal variation and individual consistency varied differently towards each novelty type, responses towards novel objects and people seem to be governed by different mechanisms. Such a degree of fluctuation has consequences for other individually consistent behaviours often measured within the nonhuman personality literature.



When animals express neophobia, or the fear of novelty, they show an aversion to an unknown risk (Greenberg & Mettke-Hofmann, 2001). Since species have been shaped over evolutionary time to avoid unknown risks, neophobia is often thought to drive species level traits such as niche breadth, home range size or dietary generalism (Greenberg, 1989, 1990, 1992; Greenberg & Mettke-Hofmann, 2001). For example, high levels of neophobia may be favoured by selection in habitats where increased wariness is beneficial for survival and reproduction, for example in predator-rich environments (Ferrari, McCormick, Meekan, & Chivers, 2015). However, elevated neophobia may also carry potential costs if increased fear inhibits innovation (Benson-Amram & Holekamp, 2012; Greenberg, 2003), or limits defences, for instance, against nest predators (Vrublevska et al., 2015). These costs and benefits of risk taking are likely to vary over time and contexts in a way that could alter the expression of neophobia. For example, it could be beneficial to adjust neophobia levels when environmental opportunities or dangers change, such as food availability or predation pressure (e.g. Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013). Therefore, animals may have evolved species-typical patterns of plasticity in neophobia if environments vary in predictable ways.

Every year environments undergo predictable seasonal cycles that trigger changes in animals' metabolism and thermoregulatory processes (Thomas, Bieber, Arnold, & Millesi, 2012). Therefore, just as seasonal change impacts behaviour related to physiological processes, neophobia levels may also change in response to the changing risks and rewards of the time of year. The extent to which species mediate their neophobia seasonally is unclear, and the

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handful of studies conducted on birds to date have generated conflicting and inconsistent findings (Apfelbeck & Raess, 2008; Mettke-Hofmann, 2007, 2000; Shephard, Lea, & Hempel de Ibarra, 2014). Moreover, it is unknown whether or not all individuals respond similarly to seasonal influences.

Individuals are commonly assumed to vary consistently in their neophobia (e.g. Bebus, Small, Jones, Elderbrock, & Schoech, 2016). In fact, neophobia is often used as a marker of nonhuman personality or temperament, because it is considered a stable response to challenges or risks across times or situations (Dall, Houston, & McNamara, 2004). However, it is unclear whether all individuals similarly mediate their neophobic behaviours under changing conditions. Such individual variation begs the question of why certain behaviours remain rigid and why others show variable plasticity (Carter, Goldizen, & Heinsohn, 2012).

Several proximate and ultimate explanations for neophobic behaviour suggest species' neophobia levels should vary seasonally, and that not all individuals may be consistent in these changes. First, changes in motivation and hormone levels throughout the year could have a powerful influence on neophobia and other types of risk taking. For example, many bird species undergo physiological and behavioural changes during the breeding season (Pdulka, Rohrbaugh, & Bonney, 2004), altering hunger and activity levels, which could contribute to changes in neophobic behaviours. Levels of stress hormones, such as corticosterone, thought to influence neophobic responses, vary by season (Romero, 2002), and often lack consistency within individuals beyond seasons (Ouyang, Hau, & Bonier, 2011). In line with these patterns, over short periods of time, neophobia measures have been shown to be highly consistent (e.g. Jolles, Ostojić, & Clayton, 2013, although see Miller, Bugnyar, Pölzl, & Schwab, 2015), while over longer timeframes such as years, they can lack such consistency (e.g. Kluen & Brommer, 2013).

Second, seasonal changes to animals' social systems could influence the risks and rewards of approaching novelty. For example, the presence of dominant individuals can alter the costs or benefits of neophobia if approaching novelty allows subordinates to circumvent competition for favoured resources, but this can depend on the species in question. In some corvid social systems, such as those of carrion crows, *Corvus corone*, dominants are more likely to take risks by approaching novelty, and subordinates benefit, at least in family groups (Chiarati, Canestrari, Vera, & Baglione, 2012). However, in other species, such as common ravens, *Corvus corax*, subordinates are less neophobic, at least around novel food, potentially approaching novelty to avoid competition with dominants (Heinrich, Marzluff, & Adams, 1995). If seasonal changes in social structure and hormone levels increase the frequency of contact and aggression between subordinates and dominants, then the risks and rewards for approaching novelty might also vary, but would do so differently depending on individuals' dominance rank. Additionally, the presence of conspecifics can influence levels of novelty approach (Miller et al., 2015), and the extent to which conspecific social cues influence behaviour can vary seasonally (e.g. Greggor, McIvor, Clayton, & Thornton, 2016). Therefore, efforts to determine the factors that influence neophobia must consider the dominance of individuals, and the social environment they occupy when assessing risk taking. By measuring neophobia within social settings that would be common in the wild (Dall & Griffith, 2014), tests are more likely to capture natural interactions between dominance, neophobia and seasonal changes to the social system.

Finally, not all types of novel stimuli elicit the same reactions, and different types of novelty may be more threatening at certain times of year. Individual measures of neophobia towards different types of novelty, such as objects and locations, do not always correlate (e.g. Boogert, Reader, & Laland, 2006; Fox, Ladage, Roth, & Pravosudov, 2009), and neophobia is not always predictive of wariness towards other threatening stimuli such as predators (e.g. Carter, Marshall, Heinsohn, & Cowlishaw, 2012). Similar to what has been proposed for other behaviours considered to be stable across time and/or contexts (Dall & Griffith, 2014), understanding the mechanisms behind neophobic behaviour requires examining it when contextual changes occur that may influence its expression. Several underlying mechanisms can contribute to the expression of neophobic behaviour, such as novelty categorization and physiological fear responses (Greggor, Thornton, & Clayton, 2015). Individual fluctuation in these mechanisms could help explain the existence and maintenance of individually varying behavioural reaction norms (e.g. Dingemanse, Kazem, Reale, & Wright, 2010). However, without an understanding of how neophobia naturally varies throughout the year, it is difficult to assess to what extent individuals might vary in their level and stability of neophobia.

We measured the risk-taking behaviour of a social group of captive rooks, *Corvus frugilegus*, towards novel objects and novel people to measure the temporal effects and individual stability of neophobia. Tests and their control conditions were run over a full year within a social group to gauge the potential effect of social rank on neophobia over time. While novel object tests are the most common measure of neophobia (Greggor et al., 2015), examining reactions to novel people allowed us to verify whether seasonal change influences novelty responses per se, or influences more ecologically relevant fear behaviours such as predatory wariness. Rooks are an excellent model species to test these dynamics because they experience seasonal changes in behaviour while breeding, are known to be very neophobic (Greggor, Clayton, Fulford, & Thornton, 2016; Jolles et al., 2013), and are likely to be able to discriminate between human faces, as other corvids do (Davidson, Clayton, & Thornton, 2015; Lee, Lee, Choe, & Jablonski, 2011; Marzluff, Walls, Cornell, Withey, & Craig, 2010). Moreover, since we tested a group from which data had previously been collected on neophobia and dominance in the context of social feeding tactics (Jolles et al., 2013), we were also able to compare selected behaviours across a 4-year period.

Our experimental set-up led to a set of four predictions. We predicted that (1) the rooks would be more likely to approach novel objects and people during the breeding season, because hunger and feeding rates increase at that time (Feare, Dunnet, & Patterson, 1974), which can increase risk taking (Damsgard & Dill, 1998). Additionally, we predicted (2) that subordinates would demonstrate lower neophobia to avoid competition with dominants (i.e. a similar situation to ravens, Heinrich et al., 1995), but expected this effect to depend on the season, as subordinates might be more willing to risk competing with dominant individuals during the breeding season. We also predicted that (3) individual consistency across seasons would differ depending on the type of novelty. Despite both stimuli being novel, reactions towards novel people may also elicit reactions of predatory wariness, which does not always correlate with neophobia (Carter, Marshall, et al., 2012), and could be subject to different seasonal pressures. Finally, we predicted that (4) individuals would not be consistent in their approach behaviour across the different types of novelty because avoidance towards objects versus people could involve different cognitive mechanisms and ecological biases whose response strength may vary independently between individuals.

## METHODS

### *Subjects and Housing*

The group of adult rooks was housed in an outdoor aviary at the University of Cambridge's Sub-Department of Animal Behaviour, Madingley, U.K. where they experienced ambient light and