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# Explaining the Paradox of Neophobic Explorers: The Social Information Hypothesis

Sofia I. F. Forss[1] · Sonja E. Koski[1,2] · Carel P. van Schaik[1]

**Abstract** How animals react to novel food and objects is commonly thought of as a crucial step toward innovations. One would therefore expect innovative species to be attracted to novelty and benefit from a combination of low neophobia and a high motivation to explore. Here we draw attention to the innovation paradox: the most innovative species tend to show neophobic reactions when confronted with novel objects or food, but can use social cues to overcome their initial neophobia. Work on novelty response has highlighted the role of ecological factors as determinants of neophobia and exploration tendency. We examine social influences on novelty response and present the idea that social factors enable some species to maintain the paradoxical combination of high neophobia and high exploration tendency. We compare primates with other species, to assess the extent to which primates are unusual. We review empirical studies that show how intrinsic neophobia is generally overcome by social facilitation and social information, i.e., the presence of experts, especially in species with slow life history, probably because social information reduces risk. We also briefly discuss the role of environmental risk in reducing intrinsic neophobia, in particular its absence in captivity. We draw attention to a strong neophobia-reducing effect of being in captivity, due to humans acting as sources of social information. We propose that species showing the paradoxical combination of strong neophobia and strong exploration tendency use social information to select aspects of the environment worth exploring. The social information hypothesis thus offers an explanation for the paradox of neophobic explorers.

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## Introduction

Response to novelty refers to the way an individual reacts to novel stimuli, such as objects, food, contexts, or environments. It is often categorized as neophobia, defined as avoidance of novelty (Barnett 1958; Greenberg 2003; Greenberg and Mettke-Hofmann 2001; Marples *et al.* 2007; Rozin 1977), or neophilia, defined as attraction toward unfamiliar things or places and a strong tendency to explore them (Brown and Nemes 2008; Corey 1979; Greenberg 2003; Heinrich 1995a). Although neophobia and neophilia are often treated as lying on a single dimension, and seen as the endpoints of the boldness–shyness continuum (Brown *et al.* 2005; Burns 2008; Frost *et al.* 2007; Wilson *et al.* 1994; Wilson and Stevens 2005), they are independently regulated motivations (Biondi *et al.* 2010; Carter *et al.* 2012; Greenberg 2003; Greenberg and Mettke-Hofmann 2001; Hughes 2007; Mettke-Hofmann 2014; Mettke-Hofmann *et al.* 2002; Miranda *et al.* 2013; Pisula *et al.* 2012; Russell 1973; Sabbatini *et al.* 2007). They are also presumably controlled by different genes (Weisstaub *et al.* 2006). We therefore consider neophobia and neophilia as distinct, independent traits and to underline this point will henceforth refer to neophilia as the tendency to explore (*exploration tendency*).

One consequence of considering neophobia and exploration tendency as independent variables is that we can examine how they can be combined. To visualize the possible combinations of neophobia and exploration tendency we dichotomized each variable as low and high (Fig. 1: after Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann 2014). We predict the kinds of species showing the four possible combinations of these variables (Fig. 1). Explanations for variation in neophobia focus mainly on ecological factors (Greenberg 2003; Sol *et al.* 2011; Webster and Lefebvre 2001; see
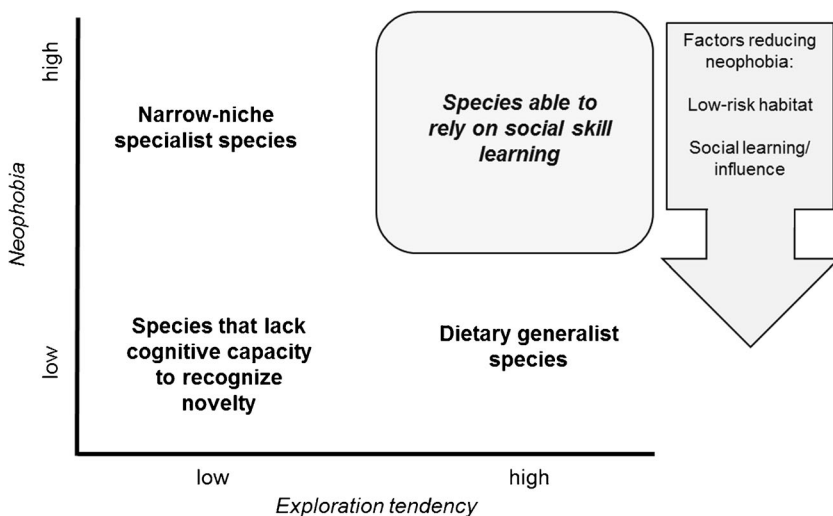


**Fig. 1** Possible combinations of neophobia and exploration tendency, with the kind of species predicted to represent each cell. (Modified from Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann 2014).

review in Mettke-Hofmann 2014). Ecology, in particular diet, provides a plausible explanation for two of the four possible combinations in Fig. 1. Dietary generalist species are reported to be less neophobic than closely related specialist species in primates (Bergman and Kitchen 2009), carnivorans (Travaini *et al.* 2013), and birds (Greenberg 1984, 1990b; Sol *et al.* 2011; Webster and Lefebvre 2001), although this is not always the case (birds: Camín *et al.* 2016). All else equal, we would expect species with a diverse and complex diet to have reduced neophobia to maximize use of their feeding niche (Greenberg 2003). This combination of low neophobia and high exploration tendency can be contrasted with the opposite combination, i.e., high neophobia and low exploration (Fig. 1), which would characterize habitat and diet specialists. The combination of low neophobia and low exploration tendency is not expected for species that can recognize novelty, because one would expect species with a positive, i.e., nonavoiding response to novelty, to subsequently also explore the novel items, unless there is no need for exploration.

Ecology does not readily explain the fourth, paradoxical combination of high neophobia and high exploration tendency. For example, primates, and some other lineages such as corvids, are cognitively flexible and highly innovative (Emery and Clayton 2004; Heinrich and Bugnyar 2005; Reader *et al.* 2011; Taylor *et al.* 2010; van Schaik *et al.* 2006a) and dietary generalists, but do not particularly seek novelty (Brown and Jones 2016; Forss *et al.* 2015). We therefore need an explanation that complements ecological explanations for variation in novelty response.

The goal of this review is to evaluate the idea that social factors, in the form of social facilitation or social information, can reduce neophobia by allowing naïve individuals to select novel items in the environment that are worth exploring (or interacting with: Sherwin *et al.* 2002), and so overcome their neophobia. According to the social information hypothesis, relying on social information is an adaptation that can selectively reduce neophobia in a social situation. We propose that over evolutionary time the opportunity to rely on social information selects for higher intrinsic neophobia in those lineages with slow life history and abundant role models, such as primates. In wild orangutans (*Pongo abelii*), for instance, cautiousness toward novelty is overcome through social cues (Forss *et al.* 2015), which then elicit a high tendency to explore (Schuppli *et al.* 2016; Schuppli *et al.* unpubl. data). Given that error-free copying would require no individual exploration, this strong exploration tendency may be particularly important in species that lack high-fidelity copying (Galef 2015; Whiten 2015; Whiten *et al.* 2016) or in situations where this is impossible. For primates in natural habitats the details of successful foraging on a novel food item are often invisible to the observer and thus once a social source has confirmed that something is not dangerous, a strong exploration tendency is needed to acquire relevant feeding innovations (Schuppli *et al.* 2016; van Schaik *et al.* 2016). In sum, a social source is needed to overcome intrinsic neophobia and draw attention to novel items worth exploring. This would explain the combination of high neophobia and high exploration tendency observed in many primates.

We first examine the functions of neophobia and exploration tendency separately, and predict that intrinsic levels of neophobia should vary depending on a species' life history and access to role models. We then review evidence for the use of social information to selectively reduce neophobia. We incorporate the role of ecology in the form of habitat risk, emphasizing the reduction of such risk in captive habitats (Fig. 1). We also ask whether social factors contribute to the observed captivity effect of

reduced neophobia. Finally we discuss the implications of social information and its influences on response to novelty in primates and other species.

## The Innovation Paradox

Animal innovation is generally defined as a new behavioral pattern learned by an individual (Ramsey et al. 2007; Reader and Laland 2003) and thus as an expression of behavioral flexibility. Low neophobia and high exploration tendency are associated with innovativeness in various studies (Benson-Amram and Holekamp 2012; Bouchard 2002; Day et al. 2003; Greenberg 2003; Lefebvre et al. 2004; Miller et al. 2016; Overington et al. 2009, 2011; Reader 2003; Seferta et al. 2001; Sol et al. 2005; Webster and Lefebvre 2001). Thus, attraction to novelty appears to be adaptive. Moreover, as innovation rates are linked to large relative brain size (Deaner et al. 2007; Lefebvre et al. 2004; Overington et al. 2009; Reader et al. 2011), large-brained species are often thought to be driven to explore novelty. All of this appears to support the notion that low neophobia is tightly linked to innovativeness.

The social information hypothesis must therefore explain how neophobic species can nonetheless be innovative. Such species exist: we see many innovations in species such as the great apes and ravens that are not particularly novelty seeking in nature (Biro et al. 2003; Boesch 1995; Brown and Jones 2016; Forss et al. 2015; Kijne and Kotrschal 2002; van Schaik et al. 2006b). The best explanation is that in species such as primates, innovations arise mostly as accidental byproducts of socially induced exploration rather than from systematic independent exploration (Koops et al. 2014), but then tend to remain in the population due to a strong preference to acquire knowledge and skills socially (van Schaik et al. 2016), which makes adults effective role models for the acquisition of innovations by young animals. The function of the high potential innovation ability (intelligence) is therefore not to explore and innovate but to acquire innovations made by others in the past as fast as possible (van Schaik and Burkart 2011), with innovations arising accidentally. Other factors such as age and rank may also cause intraspecific variation in neophobia and exploration (Biondi et al. 2010; Chiarati et al. 2012; Mettler and Shivik 2007; Thornton and Samson 2012), which will favor innovations derived directly from responding to something new. In primates, however, these represent simple innovations such as feeding on a new dietary item that does not require extractive foraging and individual practice (van Schaik et al. 2016).

## The Functions of Neophobia and Exploration Tendency

The response to novelty can affect survival. In both salmon (Salmo spp.) and swift foxes (Vulpes velox), individuals with low neophobia, assessed during rearing in captivity, experienced higher mortality after release into the wild than wild-born individuals, suggesting fitness benefits of neophobia (Brown and Laland 2001; Bremner-Harrison et al. 2004). In contrast, low neophobia can be beneficial in predator mobbing in great tits (Parus major) and thus is related to higher reproductive success (Vrublevska et al. 2015). Finally, neophobia can be unrelated to fitness, as shown in jackdaws (Corvus monedula: Greggor et al. 2017; Schuett et al. 2012). These variable outcomes suggest that the selective advantage of neophobia is affected by multiple variables.

A functional perspective on neophobia as a protection mechanism, against potentially harmful foods or predation risk during exploration, leads to two basic predictions. First, animals should avoid novelty if they can (Corey 1979), but do so less or not at all if they cannot afford to because they lack vital skills or access to resources, or if the risks are outweighed by the benefits of exploration. The *dangerous niche hypothesis* (Barnett 1958; Greenberg 2003) argues that neophobia is higher in species and individuals that are exposed to higher risks or are more likely to encounter danger within their habitats. Likewise, the *neophobia threshold hypothesis* emphasizes the exposure to microhabitat diversity early in life and its effect on how likely an animal is to avoid or explore a novel food resource (Greenberg 1983; Greenberg and Mettke-Hofmann 2001).

A second basic prediction is that life expectancy should influence the acceptable level of risk and thus variation in intrinsic levels of neophobia (van Schaik *et al.* 2006a): where life expectancy is low, acceptable risk level goes up and, consequently, neophobia decreases. Thus selection should have made species with short life expectancies and a fast life history less avoidant of novelty than those with long life expectancy. Although animals with a short life span may be under higher time pressure and therefore may have less time to explore novel foods or objects, they can be more risk prone whenever boldness brings fitness benefits, such as mating.

The life history effect should also apply within species. Individuals with low future prospects of reproduction or survival should increase their fitness potential by taking more risks to maximize energy acquisition and reproductive opportunities (Dammhahn 2012). Conversely, those with higher likelihood of survival or reproduction or slower growth should be more cautious (Biro and Stamps 2008; Dall *et al.* 2012; Kight *et al.* 2013; Wolf *et al.* 2007). We test these predictions in the text that follows.

Turning to exploration tendency, Reader and Laland (2002) suggested that it benefits individuals by leading to the acquisition of new, potentially valuable resources or knowledge. Exploration also involves costs. First, exploring potentially toxic or noxious plant parts and venomous or poisonous prey represents a direct risk, especially if they are novel and thus unfamiliar. Second, there is a tradeoff between time dedicated to exploration and other crucial activities, such as attention to predators or hostile conspecifics (Dukas 2009). Thus, exploration entails an opportunity cost, especially when explorative actions are time consuming yet unsuccessful. Thus, we can make the same basic prediction for exploration as for neophobia. An animal should explore if the risks are minimal, of if the same benefits cannot be acquired by learning from conspecifics (O'Hara *et al.* 2012) and individual exploration is therefore essential for gaining fundamental skills or access to resources.

Studies that exclusively assess exploration are rare, because low exploration tendency cannot be cleanly separated from neophobia in experiments, where exploration usually involves novel objects and food. Hence, we focus on the dependencies between exploration and neophobia.

## Social Influences on Novelty Response

The social information hypothesis predicts that animals can afford to be intrinsically more neophobic if they are social (van Schaik *et al.* 2006a, b). A social lifestyle may affect the novelty response in two different ways. First, simply being with other, equally

naïve individuals may reduce the risk of approaching novel objects because of outsourced vigilance: the cost of attention to novelty and exploration is lower when nearby animals are vigilant for predators (cf. Dukas 2009). This is thus a pure *social facilitation* effect, which also implies shared risk.

Second, the risk of a novel object being dangerous is reduced when naïve individuals, for whom the objects are novel, can rely on experienced individuals, for whom the objects are not novel (Galef 1993; Visalberghi and Addessi 2000). This therefore describes a *social information* effect and consequently, all else being equal, long association with parents or other experienced models (often linked to a slow life-history pace) would favor greater intrinsic neophobia in developing individuals because they can acquire experience through social learning, directly or indirectly (Boyd and Richerson 1985; Galef and Wigmore 1983; Galef *et al.* 1984; Laland 2004; Rendell *et al.* 2011). Individuals of species with nonoverlapping generations can still have a preference for using social information in situations where it is present (Wilkinson *et al.* 2010), but will have fewer opportunities to do so, as peers are normally equally naïve in their experiences with their habitat and any novel stimuli. Thus, if they are to explore their environment they will need low intrinsic neophobia or to rely strongly on social facilitation relative to species that live in association with the parental generation.

An effect of sociality on neophobia has been reported for a wide range of species from fish to primates (Tables I and II). A direct test of the social information hypothesis would require a broad comparison of novelty response across taxa in relation to life-history trajectories and opportunities for social learning. For now, we collated studies that have examined social effects on neophobia and exploration. We first reviewed studies addressing the independent effects of sociality per se, i.e., social facilitation, when the same individuals are tested in both solitary and social condition and all participating individuals are equally naïve (Table I). Because not all studies were designed with a control condition, where individuals are also presented novelty alone, social effects on novelty responses are likely to be more common than the results in the table suggest. Second, we examined studies in which there was an asymmetry in knowledge (and thus the items were not equally new to all individuals in the study), which allows us to distinguish the effect of association with experienced individuals: social information (Table II). We included only studies whose design permitted us to disentangle the social facilitation and social information effects. Because responses to novel space and novel items (potential food) are often uncorrelated (Boogert *et al.* 2006; Burns 2008; Carazo *et al.* 2014; Fox *et al.* 2009), we focused exclusively on responses to novel objects and potential foods.

**Social Facilitation Effects**

It has often been suggested that a social environment reduces stress when approaching novelty in a group context vs. alone (Greenberg 1990a; Moretti *et al.* 2015; Stöwe *et al.* 2006a; Visalberghi and Addessi 2000). Some studies have specifically tested this possible social facilitation effect by comparing the response to novelty of the same subjects when they were alone vs. when they were in a social context (Table I). In various primates, neophobia was overcome faster in a social setting as compared to the solitary condition (Visalberghi and Addessi 2000; Visalberghi and Fragaszy 1995; Voelkl *et al.* 2006; Yamamoto and Lopes 2004). This effect was also found for other

**Table 1** The social facilitation effect: responses to novelty in species in which individuals have been tested both alone and in a social context

| Species | Test paradigm | Test setting | Social condition reduces neophobia | Kin effect | Comments | Reference |
|---|---|---|---|---|---|---|
| *Acridotheres tristis*/mynah | Novel object | Captive | No | | When tested with conspecifics birds delayed approach to a novel object relative to when alone. | Griffin et al. 2013 |
| *Canis lupus*/wolf | Novel object | Captive | Yes | Yes | Presence of conspecifics, especially kin, reduced latencies toward novel objects. | Moretti et al. 2015 |
| *Canis familiaris*/dog | Novel object | Captive | Yes | Yes | Presence of conspecifics, especially kin, reduced latencies toward novel objects. | Moretti et al. 2015 |
| *Callithrix jacchus*/marmoset | Novel food | Captive | Yes | | Juvenile marmosets showed higher food neophobia when tested alone than in group condition. | Yamamoto and Lopes 2004 Voelkl et al. 2006 |
| *Cebus apella*/capuchin monkey | Novel food | Captive | Yes | | Consumption of novel food increased in social setting compared to when alone. | Visalberghi and Fragaszy 1995 Visalberghi and Addessi 2000 |
| *Corvus corax*/raven | Novel object | Captive | No | Yes | Birds approached novel objects faster when alone than in social condition. | Stöwe et al. 2006a |
| *Corvus frugilegus*/ rook | Novel food | Captive | Yes | | Rooks consumed more novel food when conspecific was present. | Dally et al. 2008 |
| *Crocuta crocuta*/hyena | Novel problem-solving box | Wild | Yes | | Presence of conspecific at the novel box reduced approach latencies. | Benson-Amram and Holekamp 2012 |
| *Melopsittacus undulatus*/parakeet | Novel object | Captive | Yes | | Reduced approach latencies in social situation. | Soma and Hasegawa 2004 |
| *Pachyuromys duprasi*/gerbil | Novel food | Captive | Yes | | Subjects reduced food neophobia in the presence of trained demonstrator. | Forkman 1991 |
| *Perca fluviatilis*/perch | Novel food | Captive | Yes | | Presence of trained demonstrator facilitated consumption of novel food. | Magnhagen and Staffan 2003 |
| *Sturnus vulgaris*/starling | Novel object | Captive | No | | Individuals tested alone were not more neophobic than those tested with their group. | Apfelbeck and Raess 2008 |
| *Taeniopygia guttata*/zebra finch | Novel object | Captive | Yes | | Birds in flocks were less neophobic than solitary birds. | Coleman and Mellgren 1994 |
| *Quiscalus lugubris*/carib grackle | Novel problem-solving apparatus | Captive | No | | Birds took longer to approach a novel problem-solving apparatus in a social situation. | Overington et al. 2009 |

Species are listed in alphabetical order. Blank cells indicate absence of information

**Table II** Studies examining response to novelty where the experiment presents an asymmetry in knowledge so that one naïve individual encounters the novelty together with a non-naïve participant

| Species | Test paradigm | Social cue reduces neophobia | Influential social source | Experimental paradigm | Reference |
|---|---|---|---|---|---|
| *Callithrix jacchus*/marmoset | Novel food | Yes | Adult group member | Did not consume novel food alone but did so when tested with adult group members. | Yamamoto and Lopes 2004 |
| *Corvus corax*/raven | Novel object | Yes | Human observer | Ravens approached objects faster if observing human caretaker providing the objects (no control reported). | Heinrich 1988 |
| *Corvus corax*/raven | Novel object | Yes | Kin | Subjects approached novelty faster when tested with siblings compared to nonkin. | Stöwe *et al.* 2006b |
| *Corvus frugilegus*/ rook | Novel food | Yes | Trained conspecific | Subjects would consume same food as demonstrator in novel food condition, but not in familiar food condition. | Dally *et al.* 2008 |
| *Corvus monedula*/ jackdaw | Novel food | Yes | Demonstrator from same flock | Birds more likely to consume novel food after observing a demonstrator. | Greggor *et al.* 2016 |
| *Daubentonia madagascariensis*/aye-aye | Novel food | Yes | Mother | Infants ingested food only after observing their mother. | Krakauer 2005 |
| *Eulemur m. macaco*/black lemur | Novel food | Yes | Dominant female | Dominant female present vs. absent. | Gosset and Roeder 2001 |
| *Gallus spadiceus*/ red jungle fowl | Novel food | Yes | Video of conspecific | Video showing conspecifics feeding on different food dishes and general activities near food. | McQuoid and Galef 1993 |
| *Gallus domesticus*/domesticated fowl | Novel food | Yes | Trained conspecific | Demonstrator's disgust response vs. demonstrator preference. | Sherwin *et al.* 2002 |
| *Homo sapiens*/human | Novel food | Yes | Familiar adult | Three conditions: A) adult model not eating, B) adult model eating different food, and C) adult model eating same food. | Addessi *et al.* 2005 |
| *Macaca mulatta*/rhesus macaque | Novel food | Yes | Human observer | Food found without human present vs. food given by human observer. | Johnson 2000 |
| *Pan troglodytes*/chimpanzee | Novel food | Yes | Mother | Familiar food vs. novel food. Mothers influenced ingestion of novel but not familiar foods. | Ueno and Matsuzawa 2004 |
| *Pan troglodytes*/chimpanzee | Novel problem-solving apparatus | Yes | Dominant | Subjects preferred social cue from dominants and successful individuals when engaging with a novel problem-solving apparatus. | Kendal *et al.* 2015 |
| *Rhabdomys pumilio*/striped mouse | Novel food | Yes | Mother | Mothers preferred over fathers as demonstrators. | Rymer *et al.* 2008 |
| *Salmo salar*/Atlantic salmon | Novel food | Yes | Trained conspecific | Influence of trained vs. untrained conspecific. | Brown and Laland 2002 |
| *Sus domesticus*/pig | Novel food | Yes | Demonstrator familiar | Demonstrator from same vs. different pen. | Figueroa *et al.* 2013 |

Species are listed in alphabetical order

mammal species (Forkman 1991; Moretti *et al.* 2015) and for birds (Coleman and Mellgren 1994; Dally *et al.* 2008; Soma and Hasegawa 2004). These studies were all conducted in captive settings where individuals are easily separated for testing. However, when tested in the wild, spotted hyenas (*Crocuta crocuta*) also showed significantly shorter approach latencies to a novel problem-solving apparatus if a conspecific was already present at the apparatus than when approaching alone (Benson-Amram and Holekamp 2012).

Some studies, all on birds, found no social facilitation of the novelty response. In some species the social setting did not reduce approach latencies to novelty (Apfelbeck and Raess 2008; Griffin *et al.* 2013; Overington *et al.* 2009). The null result in one study (Apfelbeck and Raess 2008) could be attributed to details of the experimental design: the test enclosure separated the focal bird from its flock with a barrier but the social group became invisible to the focal if the group flew down to the test feeder. Thus in the social condition the focal bird may have stayed away from the novelty on its own side to maintain visual contact with conspecifics. However, experimental design did not explain the results in other studies. In some cases, birds that are permanently gregarious can afford to have a tendency to simply wait for other, potentially more experienced, individuals to take the lead. This could explain the absence of social facilitation in mynahs (*Acridotheres tristis*: Griffin *et al.* 2013; Sol *et al.* 2012), and why individuals from larger groups of birds show higher neophobia than birds from smaller groups (Dardenne *et al.* 2013). Alternatively, social facilitation may be absent because scrounging is more likely in the social condition than when foraging alone (Bugnyar and Kotrschal 2002; Coolen and Giraldeau 2003; Griffin *et al.* 2013; Mathot and Giraldeau 2010; Stöwe *et al.* 2006a). In conclusion, therefore, a positive social facilitation effect on novelty response is commonly found, at least in primates, but the exceptions, found in birds, do not follow an obvious pattern.

## Social Information: Dependence on Experts

Individuals may respond differently to knowledgeable or experienced individuals compared to other, equally naïve group members, or may be especially prone to use social cues when there is an asymmetry in knowledge. Many studies suggest this preferential reliance on social information (Gunst *et al.* 2008; Jaeggi *et al.* 2010; Kendal *et al.* 2015; Luncz and Boesch 2014; Slagsvold and Wiebe 2007; van Schaik *et al.* 2006a, b). A study of orangutans (*Pongo abelii*) found that repeated exposure to a novel food item did not increase acceptance, whereas observing a conspecific consuming it did (Hardus 2012). Recent food experiments on zoo-housed chimpanzees (*Pan troglodytes*) and orangutans (*Pongo* spp.), presented with novel plants in a social setting where all individuals were equally naïve, showed that social attention to known group members was the main factor influencing ingestion of novel plant parts (Gustafsson *et al.* 2014). Although chimpanzees in a sanctuary did not attend to each other before ingesting the same novel plants, their response was both curious and cautious (Gustafsson *et al.* 2016). Without others present, these species are extremely neophobic in the wild, despite their very broad diet (Forss *et al.* 2015; Takahata *et al.* 1986).

One way to experimentally test for the social information effect is to compare an individual's novelty response in the presence of a trained demonstrator or "expert" model to its response in the absence of an experienced model. Ideally, such a test

excludes social facilitation, and thus compares the response in the presence of an experienced individual (demonstrator) with the response in the presence of an equally naïve individual. However, such tests are not common, and therefore we also included tests where there was merely a clear asymmetry in experience. Thus, we review experimental studies on reactions to novel food or objects where some individuals are regarded as "more experienced" because the item in the test is not novel to them (Table 2). All studies found that naive subjects rely on social information when given the opportunity. In domestic fowl, naïve individuals learned to avoid novel/unpalatable food through social cues from more experienced conspecifics, in part through observation of a conspecific's disgust response (Sherwin *et al.* 2002). Even in species that do not habitually associate with the parental generation, as in many fish, there is evidence that young individuals exposed to a trained demonstrator use social cues when responding to novel food (Brown and Laland 2002). We can exclude the effect of social facilitation because naïve young fish did not accept the novel food when associating with an untrained demonstrator.

In addition to experiments examining social effects on the novelty response (Table 2), both natural observations and studies of transmission biases in primates also support the prediction that specific social cues matter. Learning the feeding niche is closely associated with encountering novel things, yielding insight into the underlying mechanisms of how animals respond to novelty. Naïve individuals rely on experienced experts to guide their approach to foods that are novel to them in various primate species: lemurs (*Eulemur fulvus*: Tarnaud 2004), howlers (*Alouatta palliata:* Whitehead 1986), vervets (*Chlorocebus aethiops*: van de Waal *et al.* 2012), mountain gorillas (*Gorilla gorilla beringei*: Watts 1985), orangutans (*Pongo* spp.: Jaeggi *et al.* 2008; Schuppli *et al.* 2012), and chimpanzees (*Pan troglodytes:* Lonsdorf 2006; Luncz and Boesch 2014; Matsuzawa *et al.* 2001).

In primates, whether a naïve individual adopts a novel food or novel technique may depend on the identity of the expert. Field experiments on novel foraging techniques showed that infant vervets adopt their mother's food processing method, rather than that of other conspecifics present (van de Waal *et al.* 2014). Chimpanzees faced with a foraging problem in which two equally difficult solutions were demonstrated chose to adopt the technique performed by higher ranking or older models (Horner *et al.* 2010; Kendal *et al.* 2015). Recent studies have shown that chimpanzees also flexibly adapt a new, more efficient foraging technique when given the opportunity to watch an "expert" (Davis *et al.* 2016). However, sometimes chimpanzees copy techniques performed by subordinates, when these are the most successful ones (Watson *et al.* 2017), suggesting the additional presence of a "content bias" (Henrich and McElreath 2003).

Specific social cues also have an effect in other animal species presented with novelty. Thus, mothers are preferred over fathers (striped mice, *Rhabdomys pumilio*: Rymer *et al.* 2008), familiar over unfamiliar conspecifics (pigs, *Sus domesticus*: Figueroa *et al.* 2013), and dominant over subordinate individuals (lemurs, *Eulemur m. macaco*: Gosset and Roeader 2001; cf. Watson *et al.* 2017). Reducing risk by trusting a specific social source is supported by the observation that immature ravens (*Corvus corax*) followed a sibling toward a novel object significantly faster than they followed nonsiblings even if a social setting did not reduce neophobia (Stöwe *et al.* 2006b). Kin spent more time in close proximity and thus provided more opportunities for both learning and social facilitation (Stöwe *et al.* 2006b). Thus kin may be seen as a more reliable source of social information

than nonkin. The same pattern of faster approach in the company of kin than nonkin is also evident in canids (Table I) (Moretti *et al.* 2015).

Human children also fit the pattern of the combination of high neophobia and high tendency to explore. Children are motivated to collect information on their environment, but are nevertheless mostly unenthusiastic when presented with novel food (Pliner and Hobden 1992). Children 2.5 years of age showed a stronger avoidance of novel objects than captive great apes (Herrmann *et al.* 2011). However, because food neophobia in children is strongly influenced by the cultural environment (Birch 1995), initial food neophobia can be weakened by social influence and multiple experiences with unfamiliar food (Addessi *et al.* 2005; Birch 1980; Dovey *et al.* 2008). Children 2–5 years of age could selectively assess whether the demonstrator ate food with the same color code as they had, and accepted their novel food when this was the case (Addessi *et al.* 2005). Faced with unfamiliar food, children also prefer to rely on their mother rather than other adults (Harper and Sanders 1975). Human infants increase explorative behavior in the presence of their mother (Ainsworth and Bell 1970), implying that they rely on their mother to prevent them from exploring dangerous items.

Human children's use of social information depends on the context. Whereas younger children are more likely to accept novel food under the social influence of caregivers, adolescents attend more to social cues from peers (Shepherd and Dennison 1996). Likewise, while children tend to copy their peers in playful settings (Wood *et al.* 2016), they prefer to imitate more knowledgeable individuals in more goal-directed novel problem-solving situations (Wood *et al.* 2012, 2013). Thus, as in other primates, human children rely heavily on social information, especially from trusted role models, during the developmental phase as they learn to interact with their environment (Tomasello 1999, 2000).

Overall, the studies reviewed here overwhelmingly report an effect of the presence of trusted experts on naïve individuals' approach to novelty or ingestion of novel foods, even if its strength may vary.

## The Effect of Habitat Risk on Neophobia

Animals living in intrinsically low-risk habitats should be less neophobic (Brown *et al.* 2013; Greenberg and Mettke-Hofmann 2001; Mettke-Hofmann 2014). Indeed, in a broad comparison, island-living parrot species showed shorter latencies to explore novel objects than their mainland relatives (Mettke-Hofmann *et al.* 2002). Similarly, living in a safe habitat may explain the strongly reduced neophobia found in kea parrots (*Nestor notabilis*) living in open, high-altitude habitat (Gajdon *et al.* 2011), and in the robin (*Petroica longipes*) from Kapiti island off New Zeeland (Maloney and McLean 1995; Shaw *et al.* 2015). Such variation may also exist within species, e.g., when populations live in different habitats that vary in risk (Audet *et al.* 2015), or when captive populations are compared with wild ones.

### The Special Case of Captive Environments

Captivity presents a special case of a relatively risk-free environment, because it may also include the additional factor of there being more and/or different social models

present than available in the wild. The effect of captivity on novelty response may therefore have two nonexclusive dimensions. First, individuals living in captive conditions face drastically reduced environmental risks, which modifies an individual's learning about its environment and responses to novelty (Brown and Laland 2001; Brown *et al.* 2013). Both the degree of novelty and experience with similar stimuli, i.e., color, influence the deactivation of initial neophobia (Heinrich 1995b; Marples *et al.* 2007). Therefore, reduced neophobia in captivity may reflect a repeated lack of negative reinforcement (Haslam 2013; Kummer and Goodall 1985) and/or reduced allocation of resources to risk monitoring.

Second, in species attending to role models in their learning processes, captivity provides an additional social cue in the form of human caretakers, who may become associated with reduced risk. Consequently, orientation to humans can influence cognitive processes such as neophobia, exploration, and problem-solving ability (Damerius *et al.* 2017). The captivity effect on novelty response may be especially pronounced in species with slow life history that rely on social information, because these species show the strongest neophobia in the wild. This erosion of neophobia toward food offered by humans has been shown in semi-free-ranging conditions: macaques (*Macaca mulatta*) accepted novel food faster when it was handed to them by humans than when they merely encountered the same items in their habitat (Johnson 2000).

Alternatively, for generalist feeders, it has been argued that food neophobia is acquired after repeated experience of *conditioned taste aversion* with novel foods (Rozin 1976). However, this assumes low or even absent neophobia as the state of departure, which holds neither for primates or corvids, nor presumably for many rodents (Barnett 1958; Galef 1970; Galef and Clark 1971; Heinrich 1988; Kijne and Kotrschal 2002). Likewise, time constraints linked to a life in the wild (Kummer and Goodall 1985), which offers fewer opportunities for developing an understanding of objects and their physical affordances compared to captive life (Laidre 2007), might contribute to the captivity effect. However, wild primates regularly engage in object manipulation within their foraging niche, and although time constraints can influence the time devoted to exploring human-introduced objects, they cannot provide the whole explanation for the observed shift in interest toward novelty between captive and wild. We therefore focus on the first two possibilities: reduced risk of predation and the availability of alternative role models.

Quantitative, systematic comparisons regarding the captivity effect on novelty response exist for only a few species. Wild individuals were far more neophobic than their captive counterparts in rats (*Rattus norvegicus*: Barnett 1958; Tanas and Pisula 2011), mice (*Mus musculus domesticus*: Kronenberger and Médioni 1985), hyenas (Benson-Amram *et al.* 2013), and orangutans (Forss *et al.* 2015). Because it is unlikely that rats and mice consider their caretakers as trusted role models, the role of human caretakers may not be the full explanation. However, data on primates does suggest at least an additional role for caretaker effects. "Enculturated" apes can associate human actions with novel objects and attend to them accordingly (Tomasello *et al.* 1993; Tomasello and Call 2004) and therefore become much more explorative than their wild conspecifics. Intraspecies differences due to rearing and captivity are also reported in birds (Table III). Ravens reared in captivity approached novel animal carcasses (as well as edible and inedible inanimate novel objects) faster than wild ravens (Heinrich 1988), and also approached and interacted with any object, familiar or nonfamiliar, after a familiar human experimenter had handled it

**Table III** Species for which a captivity effect of neophobia has been reported in systematic studies comparing the response to the same novel stimulus between wild and captive or between different rearing conditions

| Species | Test paradigm | Comparison | Reduced neophobia due to human contact | Reduced neophobia in captivity | Reference |
|---|---|---|---|---|---|
| *Amazona amazonica*/parrot | Novel object | Three different rearing conditions: hand-reared, parent-reared/human-handled,parent-reared without handling | Yes | | Fox and Millam 2004 |
| *Cebus apella*/capuchin monkey | Novel object + novel food | Wild and captive (two studies - same researcher) | | Yes | Visalberghi 1988, Visalberghi *et al.* 2003 |
| *Corvus corax*/raven | Novel food | Wild and hand reared | Yes | Yes | Heinrich 1988 |
| *Crocuta crocuta*/hyena | Novel problem-solving apparatus | Wild and zoo housed | | Yes | Benson-Amram *et al.* 2013 |
| *Mus m. domesticus*/house mouse | Novel food | Wild and laboratory | | Yes | Kronenberger and Médioni 1985 |
| *Pica pica*/magpie | Novel object | Free-living and captive | | Yes | Shephard *et al.* 2015 |
| *Pongo abelii*/orangutan | Novel object | Wild and zoo individuals | Yes | Yes | Forss *et al.* 2015 |
| *Pongo abelii* \ *Pongo pygmaeus*/orangutan | Novel food + novel object | Sanctuary and zoo individuals of various rearing conditions | Yes | Yes | Damerius *et al.* 2017 |
| *Rattus norvegicus*/brown rat | Novel food | Wild and laboratory | | Yes | Barnett 1958 |
| *Rattus norvegicus*/brown rat | Novel object | Wild and laboratory | | Yes | Tanas and Pisula 2011 |
| *Vulpes velox*/swift fox | Novel object | Individuals in captivity and their survival after release to the wild | | Yes | Bremner-Harrison *et al.* 2004 |

Species are listed in alphabetical order

(Heinrich 1988, 1995a). Similarly, in orange-winged Amazon parrots (*Amazona amazonica*), hand-reared juveniles were less neophobic than the two other captive treatment groups (parent reared/ human handled and parent reared/ no handling) up until the age of 6 months. After 1 year of age all three groups showed similar levels of neophobia, which the authors ascribed to the effect of experience the birds had gathered by then (Fox and Millam 2004). We therefore suggest that species with a slow-paced life history and numerous opportunities for acquiring social information are likely to be sensitive to human provided cues in captive settings.

Socially encouraged curiosity is well documented in domestic dogs. In a setting associated with humans, dogs (*Canis familiaris*) showed a preference for novel objects when choosing between one novel and two familiar toys (Kaulfuss and Mills 2008). Domestication generally involves selection for reduced neophobia: Dogs are less neophobic than closely related wolves (*Canis lupus*), even when both are housed in similar captive settings (Moretti *et al.* 2015). Thus the same two general factors identified in the foregoing were at work in dog domestication. First, dogs living with humans generally lack negative experiences when approaching and handling novel objects in the presence of humans. Second, dogs are strongly human-oriented and see their owners as trusted experts. Dogs are better at following human actions than wolves, which primarily attend to conspecifics (Range and Virányi 2014). Domestic goats (*Capra hircus*) also use humans as sources of social information (Nawroth *et al.* 2016), suggesting that domestication may produce human-orientation effects in many species. In conclusion, the erosion of neophobia in captivity may be due to the combination of reduced negative reinforcement and the use of humans as social information sources in species that are prone to use social cues.

Reduced neophobia has been shown to improve problem-solving ability in various bird species (Auersperg *et al.* 2011; Cauchard *et al.* 2013; Sol *et al.* 2012). Likewise, captive individuals showed greater problem-solving ability than wild animals in both spotted hyenas (Benson-Amram *et al.* 2013) and orangutans (Damerius *et al.* 2017), which was attributed to both reduced neophobia and increased exploration tendency. Captive orangutans also have larger innovation repertoires than their wild counterparts (Lehner *et al.* 2010). In general, then, the captivity effect may make species that are highly neophobic in the wild and rely on social information to overcome their neophobia look like species that have low neophobia and high exploration (see Fig. 1). However, the captivity effect also shows that neophobia, although generally adaptive in the wild, comes with the opportunity cost that the species is less likely to produce sophisticated innovations and accumulate them through social transmission into cultural repertoires.

## Discussion

We found support for the idea that species in which social information is systematically available can maintain an adaptive intrinsic neophobia to avoid ecologically risky situations without suffering negative consequences. Learning from others is an adaptive strategy to avoid potentially dangerous novelty responses (Giraldeau 1997), especially when it comes to skills rather than perishable information (Reader 2015; Rendell *et al.* 2010; van Schaik 2010). The social effect on reduced neophobia comes in two forms: 1) a decrease in shared

risk (social facilitation) and 2) an asymmetric reliance on more knowledgeable, and therefore usually older, experts (social information). We examined the prediction that species with customary access to social information should show pronounced neophobia, but should engage in extensive exploration once a social source (expert, role model) has indicated that a particular context is not risky (Kendal *et al.* 2015). Social facilitation and trust in experts also allow individuals to explore because they reduce cognitive load since animals can afford to lower their vigilance toward predators and other environmental risks. The evidence reviewed here is mostly consistent with this prediction in primates and a variety of long-lived social birds and mammals.

A second major finding is that individuals living in risk-free captive habitats show lower neophobia than wild conspecifics. One reason is presumably the lack of negative reinforcement when exploring novelty. Another is that species that use social information in the wild rely on human caretakers as role models and interact with all the items these caretakers handle. The number of species that actually rely on social information to overcome neophobia may be underestimated because we would have placed these species into the same category (low neophobia-high exploration) as opportunistic generalists had we not had information on their behavior in the wild.

The combination of high neophobia and high exploration should be associated not only with tolerant sociality but also with slow life history. For young individuals, the whole world is novel, but in species with a slow life history and thus low immature mortality and long life expectancy, these immatures should not jeopardize their survival before they reach reproductive age. This is true for a variety of long-lived species with long parent–offspring associations, often including social access to other tolerant group members: great apes, capuchin monkeys, rhesus macaques, aye-ayes, spotted hyenas, and ravens (Addessi *et al.* 2005; Benson-Amram and Holekamp 2012; Benson-Amram *et al.* 2014; Chiarati *et al.* 2012; Johnson 2000). In all these species the default condition of neophobia was overcome in the presence of a familiar companion. Future work should test this effect of life history quantitatively.

In stable environments, maturing individuals of species with a slow life history should rely on social information as long as possible. A delay in natal dispersal until well after weaning is thought to be linked to the need to learn vital skills in primates (Deaner *et al.* 2003; Isler and van Schaik 2009; Schuppli *et al.* 2012), and there is increasing evidence that many birds stay with their parents after fledging (Chiarati *et al.* 2012; Drobniak *et al.* 2015). These conditions should favor higher intrinsic neophobia accompanied by a strong exploration tendency once neophobia is suppressed, and thus the novelty response may have coevolved with how young naïve individuals learn their feeding niche. The same underlying psychological mechanisms are involved in when and how to avoid the potential risk of exploring something new. The high intrinsic exploration tendency of immatures may be especially pronounced when individuals encounter novelty as a group: If adults do not show direct fear or avoidance, immatures can afford to explore novel objects that adults have classified as irrelevant and largely ignore (Biro *et al.* 2003; Benson-Amram *et al.* 2013; Fairbanks 1993; Fairbanks and McGuire 1993; Mayeaux and Mason 1998; Menzel 1966; Thornton and Samson 2012). However, we need studies that disentangle the effects of social information and age on novelty response, for example, by examining how individuals of different age categories react when solitary as well as in the presence of other animals.

It is often suggested that innovative species have low neophobia (Auersperg *et al.* 2011; Benson-Amram and Holekamp 2012; Greenberg 2003; Sol *et al.* 2002; Webster and Lefebvre 2001). Given that great apes combine large repertoires of behavioral innovations and high neophobia (Biro *et al.* 2003; Boesch 1995; Manrique *et al.* 2013; van Schaik *et al.* 2006a), this link is not universal. There may not have been enough attention paid to the effects of the novelty-response bias in innovation repertoires in species comparisons. The main reason for this lack of investigation may be that the expected correlations between brain size and innovativeness across species, in both birds and mammals, occur despite these biases (Greenberg and Mettke-Hofmann 2001; Lefebvre *et al.* 2004; Reader and Laland 2002). This in turn may have two reasons. First, species with high intrinsic neophobia lose it in captivity, and may then be more innovative on average. Second, in the wild, the highly neophobic species that rely strongly on social information have large innovation repertoires because any innovation accidentally produced is likely to be retained by efficient social transmission (Brosnan and Hopper 2014; Russon *et al.* 2009; van Schaik *et al.* 2016). Thus, not all innovative species need necessarily be novelty-seeking explorers.

In conclusion, primates, and many other social species, strongly rely on social information and occasionally on social facilitation when confronted with novelty. This allows them to be neophobic explorers with large innovation repertoires.

**Compliance with Ethical Standards**

**Ethical Note**   This review article is based on previous published empirical studies, all of which comply with the ethical guidelines of animal welfare according to respective institution and journal of their publication.

**Conflict of Interest**   The authors declare that they have no conflict of interest.

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