

Review



Cite this article: Crane AL, Ferrari MCO. 2017
Patterns of predator neophobia:
a meta-analytic review. *Proc. R. Soc. B* **284**:
20170583.
<http://dx.doi.org/10.1098/rspb.2017.0583>

Received: 17 March 2017

Accepted: 13 July 2017

Subject Category:

Behaviour

Subject Areas:

behaviour, ecology

Keywords:

fear, noetic, novelty, predation, risk,
uncertainty

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Electronic supplementary material is available
online at [https://dx.doi.org/10.6084/m9.
figshare.c.3835972](https://dx.doi.org/10.6084/m9.figshare.c.3835972).

Patterns of predator neophobia: a meta-analytic review

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Neophobia, the fear of novel stimuli, plays a major role in animal ecology. Here, we review studies on predator neophobia and explore its underlying patterns within an ecological framework. Predator neophobia is typically assessed by observing behaviours in novel areas that bring potential risk from unknown predators, or by observing behaviours towards certain kinds of objects and odours that are novel. We conducted a literature review across taxa, surveying research on baseline and induced neophobia versus controls. We calculated effect sizes for the intensity of neophobic responses, and categorized data according to six factors (taxa, age class, background type, trophic position, test cue type and experimental treatment type). While accounting for each of the other factors, we found that baseline neophobia was stronger among birds and mammals, and towards novel areas, relative to other taxa and cue types. Baseline neophobia was lower for wild-caught animals and for those that were higher in trophic position, compared with those reared in captivity and from lower trophic levels. By contrast, induced neophobia was similar in intensity across taxa, background types and testing cue types, while again being lower among upper trophic-level members and among juvenile animals. Although induced neophobia occurred across all treatment types, brain lesions induced stronger neophobia than predation risk or social isolation. We discuss potential mechanisms underlying these results and highlight gaps in the literature.

1. Introduction

A fundamental goal in ecology is to understand the way organisms respond to various environmental stimuli via different sensory systems [1,2]. Such responses shape intra- and interspecific interactions, spatial distributions and the probability of survival [3], making appropriate responses towards stimuli critically important [4,5]. However, at the individual level, all cues are novel upon their first encounter, which can lead to uncertainty about the optimal way for an individual to respond [6]. While some species display evolved, innate responses to certain cues [7], the majority lack such a programmed response to novel cues in many contexts. Positive responses (e.g. attraction) towards novel stimuli are generally referred to as 'neophilia' [8], whereas the term 'neophobia' describes negative responses [9]. Russell Greenberg was a pioneer of research on the ecological role of neophobia [10], defining it as the degree of aversion towards novel objects or new situations, or the avoidance of an environmental element because it has not been experienced previously [11]. The term 'neotic' has also been used in this manner (e.g. [12]).

From an ecological perspective, we can group neophobia into three basic types: gustatory, social and predator neophobia. By far the most commonly studied is gustatory neophobia, where animals (including humans) demonstrate aversion towards consuming novel foods even when palatable (reviewed in: [12,13]). Thus, the avoidance of the food is due to neophobia, which can be a mechanism for reducing the risk of ingesting toxins [14]. Much less attention has gone towards

social neophobia, or fear of novel interactions with conspecifics, typically in competitive or aggressive contexts (e.g. [15,16]). However, here we review studies on predator neophobia, which we argue is a fearful reaction towards novel stimuli that are perceived as potential predation threats, and not gustatory or social threats. While some research has assessed the underlying hormonal [17] and neurophysiological [18] basis of neophobic responses, our intent here was to explore factors that potentially influence neophobic behaviour.

2. Predator neophobia overview

The risk posed by predators has a major influence on prey [19]. Fearful responses towards risky stimuli are essential for survival, but responding fearfully towards non-threats brings costs such as reduced time spent foraging or mating [20]. Thus, fitness is optimized by responding with fear only in dangerous situations. Stimuli indicating risk vary in type (e.g. visual or chemical) and in timing (before, during or after an attack) [21]. When a stimulus is novel, an animal may demonstrate neophobia because it perceives the stimulus as a possible predation threat [22]. Many animals show fear in novel spaces or areas (electronic supplementary material, table S1) where the environment is potentially dangerous due to unknown predators. If no unfamiliar food or any competitors are present, we can assume that these neophobic responses are predator neophobia. Predator neophobia is also commonly directed towards novel objects, which typically provide visual, chemical and tactile cues. When these objects are unlike food or competitor cues, animals can perceive them as potential predators. Novel objects can also represent structural features of a habitat, and thus object and spatial neophobia are sometimes intertwined. Many studies also demonstrate neophobia towards odours, and in the absence of visual or tactile information (electronic supplementary material, table S1). Again, if these odours do not mimic food or competitor odours, they can be perceived as a predator threat. Importantly, two recent studies showed that neophobia is not sensory specific [23,24]; when animals had experience with only chemical cues from a predator attack, they became neophobic towards non-chemical stimuli (visual or mechanical cues).

There is substantial individual variation in the intensity of predator neophobia [25,26]. Often, some individuals will show weak or even no neophobic responses (e.g. [27,28]). However, observations of high levels of neophobia are repeatable and can correlate across contexts (e.g. decreased use of structure and poorer problem solving [29,30]). Likewise, numerous studies have explored variation in predator neophobia across populations and species (e.g. [31,32]). Greenberg [11] proposed the 'neophobia threshold hypothesis' (figure 1a) to explain how neophobia is linked to the ecological plasticity of species. According to this hypothesis, neophobia is largely genetically based, being shaped by natural selection. A neophobic species has a lower probability of exploring new resources and shifting its niche to incorporate such. Evidence for this hypothesis comes from species that are habitat generalists showing lower levels of neophobia than habitat specialists (e.g. [36,37]).

The 'dangerous niche hypothesis' is an alternative view that the primary benefit of neophobia is protection against danger [33,38]. According to this hypothesis, animals should exhibit greater caution in riskier habitats (figure 1b). Greenberg [33] saw the dangerous niche hypothesis as conflicting with the

neophobia threshold hypothesis, but the application of these hypotheses may depend on the ecological context (e.g. the type of neophobia or the species). While the dangerous niche hypothesis has traditionally been applied to avoiding the consumption of dangerous foods, a growing body of the literature supports its application to predator neophobia. Brown *et al.* [22] fortified this paradigm by demonstrating that neophobia was a plastic trait within individuals, being induced by exposure to a high-risk environment. In that study, fish and amphibians became neophobic following repeated exposure to injured conspecific cues (hereafter 'alarm cues') that are released during a predator attack, and are innately recognized by conspecifics, reliably indicating risk [39].

Neophobia has an important adaptive role, as being frightened by novel stimuli should be beneficial in high-risk environments where novel stimuli are more likely to be dangerous. Hence, neophobic animals may avoid deadly encounters with novel predators, and benefit from increased survival. From an evolutionary perspective, phenotypically plastic neophobia [22] helps animals survive their initial encounters with novel predators (e.g. [40,41]), and can facilitate the retention of information learned from the encounter [42].

A neophobic phenotype can also allow animals to avoid the costs of learning specific information (e.g. potential death from direct information; costs of travelling, sampling and vigilance; ATP drain; and the potential cost of learning something inaccurate). However, being neophobic must also incur costs, else it would be a universal trait. M.C.O.F., D. T. Warren, M. I. McCormick & D. P. Chivers (2016, unpublished data) documented costs of neophobia in a predator-free environment where neophobic damselfish, *Pomacentrus chrysurus*, were poorer competitors compared with non-neophobic individuals. In a study on neophobic rats, *Rattus norvegicus*, a 20% increase in stress-related mortality occurred [43]. In addition to the energetic cost of a highly vigilant state, it also reduces time allocated to other fitness-related activities. These costs are preferable to being consumed, but if the chances of being consumed are low, as in safe environments, neophobia becomes maladaptive.

3. Methodological considerations

Different variations of 'open-field tests' are often used to assess neophobia (e.g. [44]). These novel environments pose unknown risk, heightened by the absence of habitat refuge. Two types of open-field tests are standard in assessing neophobia in murines. The 'free exploratory paradigm' [45] allows test subjects to move freely among familiar compartments containing bedding, before a divider is removed, opening novel, empty areas for exploration (electronic supplementary material, figure S1a). In this type of arena, a common behavioural response is 'rearing', where the test subject lifts its upper body and stands on its hind legs (e.g. [45]). This reaction can be a defensive response towards novelty (often termed 'attempts'), or it can be an exploratory behaviour (often termed 'rears'). In a different manner, the 'elevated plus maze' is a four-armed arena, taking the shape of a plus (+) symbol, where only two arms are enclosed by walls [46] (electronic supplementary material, figure S1b). Neophobic individuals are unlikely to use the open (unenclosed) walls, because the perceived risk from predators is higher (e.g. from raptors). One consideration when using choice designs such as these is that data recorded in one area should not be viewed as a control for another area

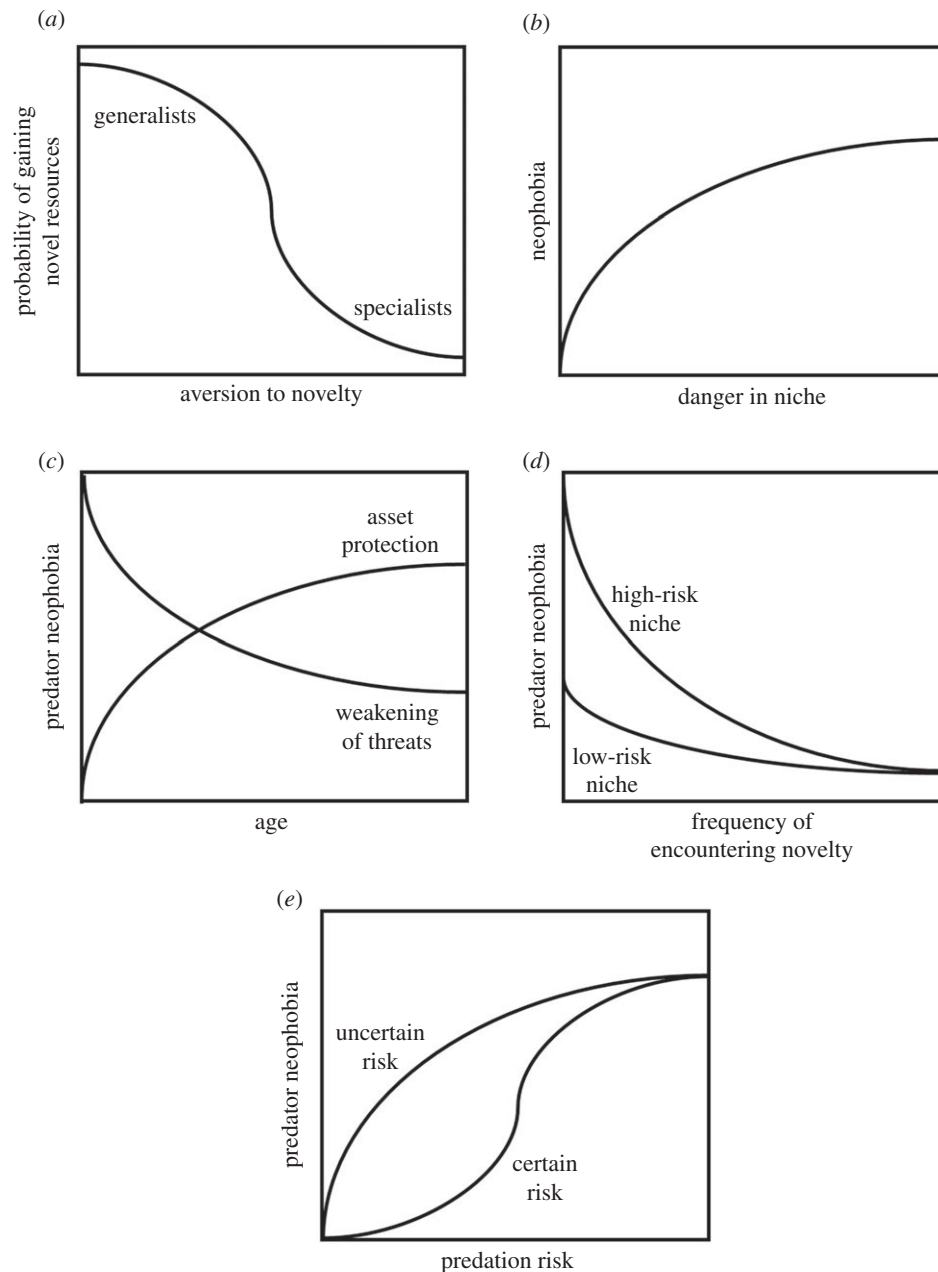


Figure 1. (a) The 'neophobia threshold hypothesis', adapted from Greenberg [11], predicting that the probability of gaining novel resources depends on aversion to novelty, whereby generalist species are less neophobic and gain novel resources more than specialist species. (b) The 'dangerous niche hypothesis', adapted from Greenberg [33], where neophobia increases with the level of danger in the niche. (c) Theoretical model where neophobia decreases with age in some species as threats become less dangerous versus a model where species become more neophobic with age because they have more assets to protect [34]. (d) Theoretical effect of the frequency of novelty on predator neophobia in high- and low-risk environments in the context of the 'risk allocation hypothesis' [35]. (e) Theoretical model for how neophobia in animals that are certain about risk may be influenced by a risk threshold.

because the times spent in each area are not independent. For example, in the free exploratory paradigm, the ideal control is an arena where both options are familiar.

Studies on object neophobia use objects such as balls, cones and blocks, although there is wide variety (e.g. [47,48]). Object neophobia is often defined as avoidance of the object resulting in decreased foraging behaviour towards a familiar food source. Other neophobic responses include reduced overall activity and increased social grouping. These variables are also standard measures of neophobia towards novel odours (e.g. [22]). Several studies have compared object neophobia across species, sometimes suffering from a lack of a control group. If, for example, species A moves less than species B in the presence of a novel object, we should not necessarily conclude that species A is more neophobic; species A may simply

be less active overall, even in the absence of the novel object. Additionally, many studies use designs where animals are tested before and after the presentation of a novel cue. In such cases, using the before period as a control is not ideal because time becomes a confounding factor. For example, if test subjects are observed feeding before and after the presentation of a novel object, they could become satiated and feed less over time, or gain information about the food and forage more over time, and thus an independent control group (familiar or no object) is needed. Finally, in studies on inducing neophobia, a control (familiar cue or no cue) may not be necessary if neophobic responses are significantly induced relative to baseline neophobia. However, if the inducing treatment were to have no effect, we are left to wonder if the treatment was ineffective or whether test subjects were already highly neophobic.

When assessing neophobia, it is fundamentally important to use a stimulus that is completely novel. Even if an animal has never encountered a specific cue, certain features of the cue may match something already feared. For example, the shape of an object may look similar to a known predator (e.g. raptors or snakes [48,49]). Likewise, an odour from a novel animal species may not be perceived as novel when test subjects have experience with odours from closely related species. This recognition paradigm is referred to as 'generalization' [50], often occurring within the same genus and family [51,52]. Thus, when researchers assess neophobia, they should use cues outside the taxonomic frame of generalization. Even when animals are taxonomically distant from the novel cues, the cues may not be evolutionarily novel [53,54]. Many animals possess innate responses to cues from predators due to coevolution (e.g. [55,56]). In such cases, the cues are not completely novel because selection has yielded individuals that recognize and respond to the cues without having individual experience.

4. Literature search and meta-analysis

Our goal was to understand factors that drive the intensity of predator neophobia, categorizing studies according to taxonomic class, age (adult or juvenile), background type (wild-caught or captive-reared), trophic position, testing cue type (e.g. area, object or odour) and any inducing treatment type (e.g. social isolation, brain lesion or exposure to predation; table 1). We used Web of Science to locate studies, searching for 'neophobi*', 'neotic', 'fear of novel*', 'background risk', 'innate response' and 'innate recogni*' within the titles of articles published between 1960 and September 2016 (approx. 4000 results). Over 75% of the results were on innate immunity, which in many instances is neophobia at the molecular level, but here our focus was on the responses of organisms. Of the remaining results, about 200 articles were related to predator neophobia, which we scanned for certain criteria. We viewed spatial, object and odour neophobia as forms of predator neophobia. One exception was object neophobia directed towards containers of food, and thus relating more to gustatory neophobia. We excluded data for responses towards cues that were not evolutionarily novel. However, many studies on innate responses to predator cues also used non-native control cues or prey from populations that were allopatric with the predator, which we included when gene flow was presumably low or absent. We also did not include obvious cases of generalization to novel cues from a known congener, and studies involving live predation through time, being novel only at the initial encounter. Furthermore, studies presenting data on multiple species combined were not included, as it was unclear whether all species had the same response pattern; if some species were neophobic and others were neophilic, the combined data would indicate no overall response. Additionally, several studies on animal personality could not be included as they assessed correlational patterns of neophobia without making group comparisons. Finally, studies were excluded when lacking a control group (familiar cue or no cue) or when no variance in neophobia was provided (required for calculating effect sizes). In total, 89 datasets from 52 studies were used in the meta-analysis, including a few studies that were outside our search results but were

found during opportunistic searching (see the electronic supplementary material, table S1 for the full list of literature).

Means and variances were extracted from tables or graphs using ImageJ 1.50i. When medians were reported alongside quartiles or maxima/minima, we used Wan *et al.*'s [57] methods for estimating parametric values. However, the number of response variables reported within each study typically ranged from one to four. This was potentially problematic because studies presenting only one response variable may not have reported weaker responses (or simply not measured them), whereas studies reporting multiple response variables may have reported excess measurements irrelevant to the anti-predator response. We sought a clearly defined rule for comparing data across studies and chose to use the strongest response within each study. Our rationale for this was that we wanted to determine what drives the intensity of a neophobic response while avoiding the aforementioned inconsistencies across studies. Extracted data were entered independently for each level of each factor (e.g. data from a study testing neophobia in a novel area and again towards a novel object were entered separately).

To calculate effect sizes for each comparison, we used Hedges's *g*, which is ideal for the instances of small sample size [58] occurring in some studies. When sample sizes were presented as ranges, we used the mean. Because neophobic responses were bidirectional across studies (i.e. higher or lower values could indicate neophobia), we adjusted Hedges's *g* for direction by reversing the sign when higher values of the response variable indicated neophobia. Because these values were both positive and negative, we used the log-modulus transformation for homoscedasticity [59]. These transformed values represented a neophobia score where higher values equate to more intense neophobia.

We assessed two types of neophobia: (i) baseline neophobia, where we compared uninduced neophobic responses with controls (familiar cues or no cue); and (ii) induced neophobia, where we compared induced neophobia with baseline neophobia. Because quantitative information regarding factors (table 1) was often not reported, we used a categorical approach. We decided against using a multiway statistical approach, because most interactions could not be tested due to lack of replication for factor combinations across studies. Instead, we adjusted each factor to account for the influence of the others using estimated marginal means. We then tested for differences with one-way ANOVAs, using Bonferroni corrections for post-hoc multiple comparisons. We used $\alpha = 0.05$ and conducted analyses in SPSS 23.

5. Patterns of neophobia

(a) Taxonomic class

Electronic supplementary material, table S1 provides the full list of studies included in the meta-analysis by taxa, with factor classifications and effect sizes. In summary, baseline levels of neophobia have been widely documented in mammals, birds, amphibians and fish, and occasionally reported in invertebrates. Neophobia appears to function similarly across taxa, as fear neural pathways have been phylogenetically conserved [60]. However, birds show the highest levels, followed by mammals ($F_{5,38} = 9.34$, $p < 0.001$; figure 2a). Perhaps differences in life-history strategies play a disproportionate role across taxa. For example, in this

Table 1. Details for the categorization of factors assessed in meta-analyses.

factor	description
taxonomic class	Based on phylogeny.
age class	'Adults' and 'juveniles' were grouped according to the test subjects' age at testing versus their age at sexual maturity. Field studies involving mostly adults were classified as adult.
background type	Animals that were wild-caught and tested in a laboratory environment, and those tested in the wild, are referred to as 'wild-caught', versus 'captive-reared' individuals that were born in captivity or removed from their natural environment immediately after hatching. Farm-raised animals were classified as captive-reared due to an absence of a natural predator landscape.
trophic position	'Tertiary' refers to animals that consume other carnivores, whereas 'lower' represents those that do not.
testing cue type	Testing cues were categorized as 'novel area', 'novel object', 'novel odour' or 'novel sounds' (vibrations).
inducing treatment type	Inducing treatments were brain lesions, drugs (e.g. stimulants such as amphetamines), castration, social isolation and exposure to predation risk in some form (e.g. alarm cues).

analysis birds generally had smaller clutch sizes than fish, amphibian and mammal species. While speculative, neophobia may be more pronounced among K-selected species, relative to r-selected species, because the loss of individual offspring is proportionally greater for species with smaller clutches. In contrast to baseline neophobia, induced neophobia appears similar across taxa ($F_{3,21} = 0.31$, $p = 0.86$; figure 3a).

(b) Age class

One might predict increased neophobia among younger animals that are less experienced and must contend with more frequent and severe threats (figure 1c). However, younger animals must also typically spend more time foraging (e.g. [61,62]), and may have less to lose in comparison with adults with offspring and territory (asset-protection principle [34]), suggesting neophobia would correlate positively with ontogeny, as found in guppies, *Poecilia reticulata* [63]. The meta-analysis revealed that, across studies, adults and juveniles did not differ significantly in baseline neophobia ($F_{1,38} = 2.19$, $p = 0.15$; figure 2b), whereas induced neophobia was significantly stronger among adult animals compared with juveniles ($F_{1,21} = 4.37$, $p = 0.049$; figure 3b). In a direct internal comparisons, Velley *et al.* [64] found similar levels of induced neophobia between different ages of adult rats, *R. norvegicus* (approx. 10 versus 13 weeks old). However, in differently aged cichlids, *Amatitlania nigrofasciata*, younger individuals showed higher levels of induced neophobia, whereas the oldest individuals showed no neophobia [65].

(c) Background type

Wild-caught animals, presumably having experience with natural predators, showed significantly lower levels of baseline neophobia than those without such experience ($F_{1,38} = 7.46$, $p = 0.01$; figure 2c). Potential explanations for this outcome are that neophobic individuals are caught less often for testing, or that in some cases directional selection against neophobia lowers the proportion of neophobic individuals within a test population. Another possibility is that neophobia lessens with increasing exposure to stimuli (figure 1c), which is more common in an ecological setting. In comparison with baseline levels, induced neophobia was similar between background types ($F_{1,21} = 0.02$, $p = 0.88$; figure 3c).

(d) Trophic position

Tertiary consumers showed significantly weaker baseline neophobia than lower-level consumers ($F_{1,38} = 10.68$, $p = 0.002$; figure 2d), supporting our hypothesis that animals of higher trophic position have less reason to show predator neophobia compared with those with more predation pressure in lower trophic levels. Induced neophobia was also significantly weaker among tertiary consumers ($F_{3,21} = 12.92$, $p = 0.002$; figure 3d) despite their lower baseline neophobia. For species of higher trophic position with fewer predators, the costs of neophobia probably outweigh the benefits.

(e) Test cue type

Baseline neophobia was strongest when tested in novel areas, intermediate towards novel objects, and weak towards novel odours and sounds ($F_{3,38} = 16.89$, $p < 0.001$; figure 2e). Although statistically significant, the small sample size for area testing may be unreliable. However, neophobia towards odours was clearly weaker than towards objects, perhaps due to the prevalence of novel odours. From a cost/benefit perspective, responding to every novel odour might bring increased costs accruing from over-responding, whereas novel areas and objects might be rarer, making incorrect neophobic responses less costly. Again, induced neophobia relative to baseline levels occurred similarly across testing cue types ($F_{5,21} = 1.34$, $p = 0.29$; figure 3e).

(f) Inducing treatment type

Studies demonstrate a variety of methods for inducing neophobia (electronic supplementary material, table S1). We found that brain lesions cause more severe neophobia than predation cues or social isolation, whereas castration and stimulant drugs cause intermediate levels ($F_{4,21} = 5.05$, $p = 0.005$; figure 3f). However, a fundamental aspect of neophobia induced by risk exposure is that higher levels of background risk cause higher levels of neophobia [66]. This principle probably applies to other inducing methods (e.g. larger versus smaller lesions or longer versus shorter social isolation), making cross-treatment comparisons difficult. A few studies have compared neophobic responses induced by risk versus responses towards known predator cues, finding either similar outcomes [22,67] or that neophobic responses were weaker [22,68].

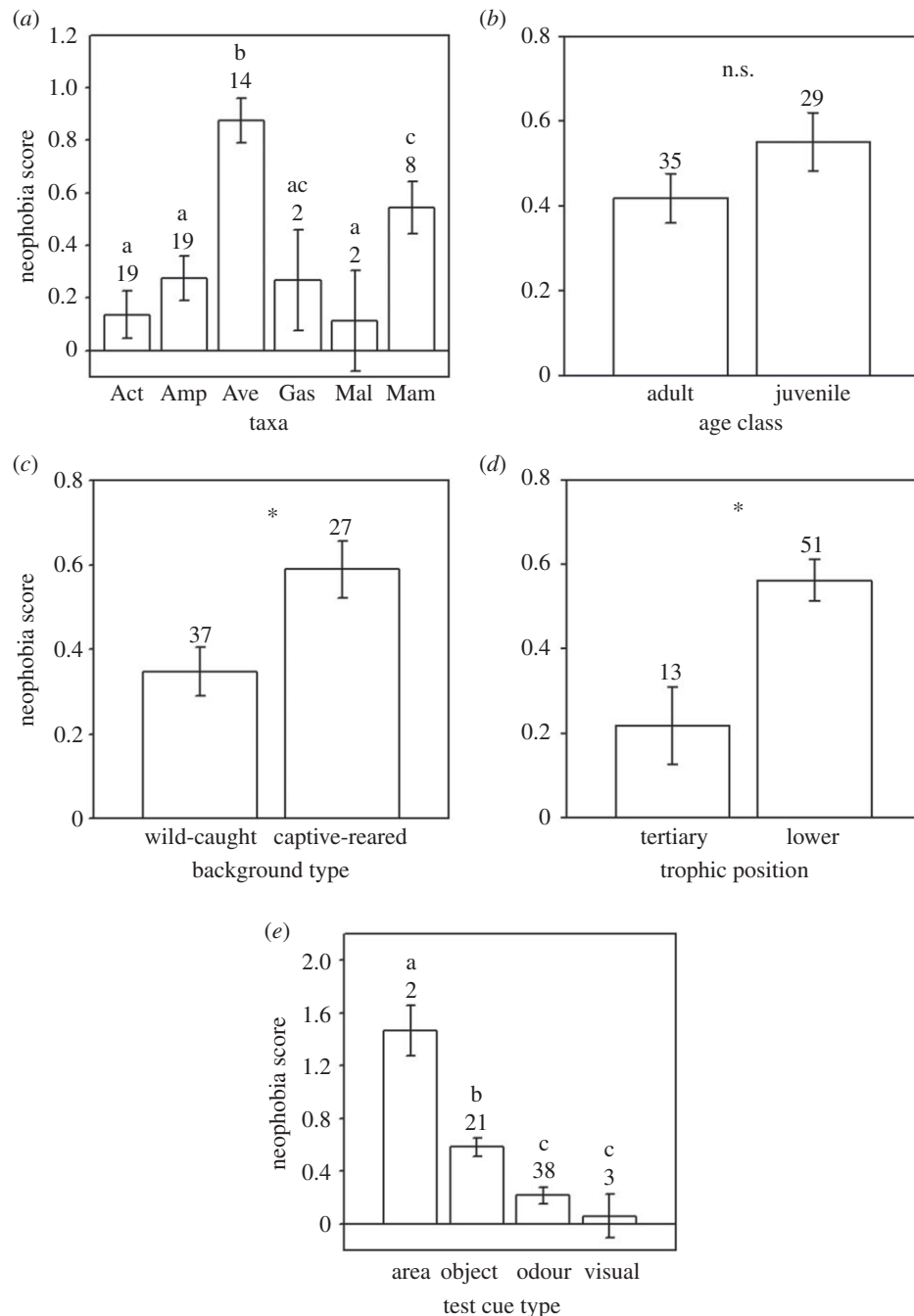


Figure 2. Estimated marginal means (\pm s.e.) for baseline neophobia scores by (a) taxa (Actinopterygii, Amphibia, Aves, Gastropoda, Malacostraca, Mammalia), (b) age class, (c) background type, (d) trophic position and (e) test cue type. Numbers above bars represent data replicates. Asterisks indicate significant differences, and bars sharing the same letter are not statistically different (n.s., non-significant). The neophobia score compares levels of each factor independently of other factors (i.e. not the raw/uncorrected levels of neophobia).

6. Other potential factors

Only a few studies have explored the role of dominance status and sex on neophobic responses. Some show that lower-ranking individuals are less neophobic than dominant individuals (e.g. [69,70]). One explanation for this pattern is that dominant individuals limit access to resources for subordinates, which forces subordinates to explore novelty. However, subordinate starlings, *Sturnus vulgaris*, were less neophobic than dominant individuals only when in their social group (i.e. not alone), suggesting that rank-dependent responses are affected by the social context [71]. By contrast, exploratory responses of novel objects by dogs, *Canis familiaris*, were rank-dependent only when dogs were alone, and lower-ranking individuals were more neophobic than higher-ranking individuals [32]. Similarly,

subordinate coyotes, *Canis latrans*, showed more neophobia than dominant individuals [72], whereas among wolves, *Canis lupus*, no rank dependency was found [32]. Mettler & Shivik [72] hypothesized that artificial removal of bold animals (via trapping or domestication) plays a role in how dominance rank influences neophobia for some species because lower-ranking individuals are no longer forced to explore novelty.

The sex of the animal can also influence neophobia. Male mice, *Mus musculus*, showed less neophobia than their female counterparts [73], and in male hamsters, *Mesocricetus auratus*, neophobia was induced by castration but was over-ridden by implanting testosterone [74]. Testosterone may also underlie dominance relationships (e.g. [75]), so the role of dominance and sex on neophobia may be intertwined. Overall, little is known about sex differences in neophobia.

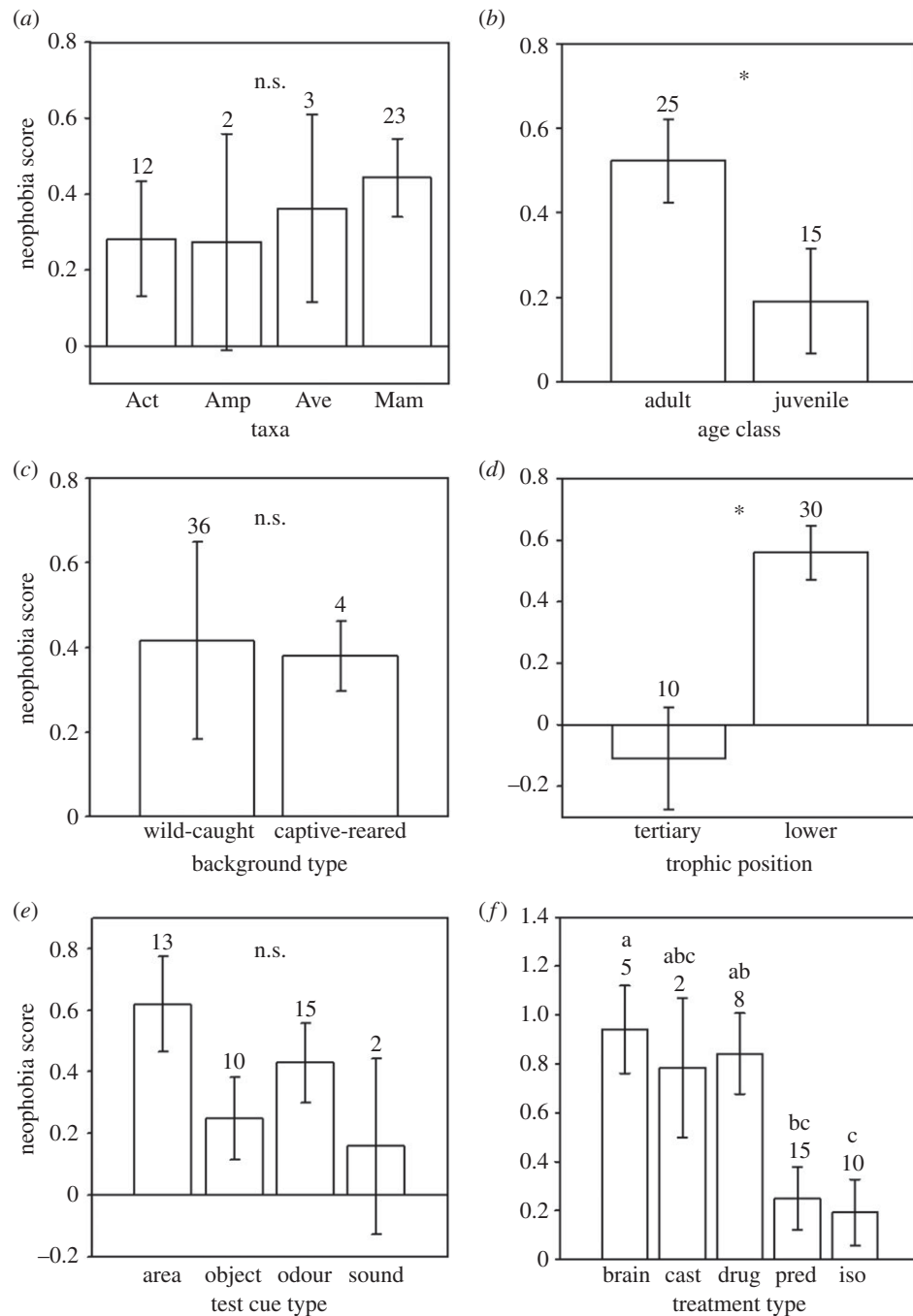


Figure 3. Estimated marginal means (\pm s.e.) for induced neophobia scores. Details are as in figure 1, with the addition of the inducing treatment type (brain lesion, castration, drugs, predation-related cues, isolation). (a) Act, Actinopterygii; Amp, Amphibia; Ave, Aves; Mam, Mammalia.

7. The longevity of neophobia

If risk ceases and the environment becomes safe, the intensity of neophobia should start to wane. While current data are too limited to include waning time in this analysis, a few studies have assessed different time points in a post-risk environment. In cichlids, *A. nigrofasciata*, the intensity of neophobia persisted for 14 days following repeated exposure to alarm cues [76], and in macaques, *Macaca fascicularis*, neophobia persisted for eight months after social isolation [77]. Neither study tested neophobia at later times, so the persistence of neophobia was unknown. However, in another experiment with cichlids, *A. nigrofasciata*, post-risk individuals showed induced neophobia 1 day later but not 21 days later [65]. Likewise, darters, *Etheostoma caeruleum*, remained neophobic for 2 days but not for 32 days [78]. In a study on

rats, *R. norvegicus*, inducing neophobia with a brain lesion caused no reduction in neophobia 4 days versus 4 weeks later [64]. As mentioned previously, the waning time of neophobia will shift depending on the intensity of the inducing treatment [66].

Although counterintuitive, neophobia should also weaken when environmental risk remains high for long periods. According to the 'risk allocation hypothesis', when risk is perpetual, animals need to ignore risk to undertake other fitness-related activities [35]. Thus, we might expect a pattern where neophobia decreases as novelty increases, as suggested in some studies on parrots, *Amazona amazonica* [79,80]. Neophobia in high-risk individuals may begin to match (or even drop below) that of low-risk individuals (figure 1d). However, in a study using social isolation to induce neophobia in macaques, *M. fascicularis*, no weakening

of the response was observed after two relatively long inducing periods (6 versus 12 months) [77]. The maximal time frame reported for the inducing period via alarm cues is only 7 days (e.g. [65]), but members of a high-risk population of guppies, *P. reticulata*, show a neophobic response in the wild [22], although it is unknown how the intensity of neophobia changes over their lifespans.

In contrast to neophobia weakening through time, we might expect neophobia to persist at high intensities when animals face infrequent or irregular bouts of risk. Ferrari *et al.* [81] induced neophobia in tadpoles, *Lithobates sylvaticus*, using alarm cues at two different times of day (morning or evening). Individuals that experienced risk during the morning became neophobic only during the morning, and vice versa. Thus, tadpoles appeared certain that novel cues were non-threatening when occurring outside the time frame of their background risk (i.e. certainty can decrease neophobia). In a subsequent study, individuals repeatedly exposed only to alarm cues became neophobic, unlike those that were knowledgeable about the predator species causing the attacks via repeated exposure to alarm cues paired with the odour of the predator [82]. However, guppies, *P. reticulata*, from a high-risk population have consistently demonstrated neophobia despite being knowledgeable about their natural predators [22]. Likewise, in a study on minnows, *Pimephales promelas*, individuals responded with the same neophobic intensity irrespective of whether they were 'certain' (alarm cues + predator odour) or not (alarm cues only) [67]. One explanation for neophobia among individuals that were certain is that, while being knowledgeable about the identity of their predator, they remained uncertain about when or from where the danger would occur. Another possibility is that the level of risk interacts with certainty, where individuals that are certain only show high levels of neophobia after a threshold of risk has been reached (figure 1e).

8. Future directions

Predator neophobia is a topic of growing interest, and many gaps in our knowledge remain. Indeed, data are limited for many of the factors assessed herein, while many other potential factors (e.g. differences between sexes or among various life-history strategies) could not be assessed due to the scarcity of data. Some taxa, such as reptiles and invertebrates, have received only rare attention, as has neophobia towards sounds. Few studies have assessed varied amounts of novelty or induced neophobia over long durations. Future work should continue to target the contexts in which neophobia occurs, while carefully choosing novel cues and control treatments that confirm responses are truly neophobic.

As the world changes through physical alteration to habitats and species invasions, animals may be more likely to encounter novel cues, or familiar cues under novel circumstances. How will animals respond to novelty and what role will neophobia play? Will neophobia benefit species facing new threats, or will it add costs without a survival benefit? Will more frequent exposure to novelty weaken neophobic responses that are critical for survival? Predicting the intensity of neophobia may become increasingly useful for species management (e.g. enhancing food production and pest control), as well as for conservation efforts that rear and release animals to replenish natural populations. Future work should continue to target how neophobia about predators shapes the ecology of prey in a changing world.

Authors' contributions. Both authors developed this review and wrote the manuscript. A.L.C. extracted data and conducted analyses.

Competing interests. We have no competing interests.

Funding. The Natural Sciences and Engineering Research Council of Canada provided a Discovery Grant to M.C.O.F. and a Vanier Scholarship to A.L.C.

Acknowledgements. We thank Bob Clark, Joe Stookey and Douglas Chivers for feedback on the manuscript.

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