CONTRIBUTED PAPERS

Savviness of prey to introduced predators

Arian D. Wallach[1] | **Daniel Ramp**[2] | **Ana Benítez-López**[3] | **Eamonn I. F. Wooster**[2] |
Scott Carroll[4] | **Alexandra J. R. Carthey**[5] | **Erin I. E. Rogers**[6] | **Owen Middleton**[7] |
Kyle J. A. Zawada[2] | **Jens-Christian Svenning**[8,9] | **Ella Avidor**[1] | **Erick Lundgren**[8,9]

[1]School of Biology and Environmental Science, Faculty of Science, Queensland University of Technology, Brisbane, Queensland, Australia

[2]Centre for Compassionate Conservation, TD School, University of Technology Sydney, Ultimo, New South Wales, Australia

[3]Department of Zoology, Faculty of Sciences, University of Granada, Granada, Spain

[4]Department of Entomology and Nematology, University of California Davis, Berkeley, California, USA

[5]Department of Biological Sciences, Macquarie University, North Ryde, New South Wales, Australia

[6]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia

[7]School of Life Sciences, University of Sussex, Brighton, UK

[8]Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus, Denmark

[9]Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus, Denmark

Correspondence
Arian D. Wallach, School of Biology and
Environmental Science, Faculty of Science,
Queensland University of Technology, Brisbane,
QLD, Australia.
Email: a.wallach@qut.edu.au

Article Impact Statement: The prey naivety
hypothesis, which is foundational to the view that
introduced predators are a threat, is unsupported by
available research.

Funding information
Australian Research Council, Grant/Award
Numbers: DP180100272, FT210100243; Junta de
Andalucía, Grant/Award Number:
EMERGIA20_00252; VILLUM FONDEN,
Grant/Award Number: 16549

Abstract

The prey naivety hypothesis posits that prey are vulnerable to introduced predators because many generations in slow gradual coevolution are needed for appropriate avoidance responses to develop. It predicts that prey will be more responsive to native than introduced predators and less responsive to introduced predators that differ substantially from native predators and from those newly established. To test these predictions, we conducted a global meta-analysis of studies that measured the wariness responses of small mammals to the scent of sympatric mammalian mesopredators. We identified 26 studies that met our selection criteria. These studies comprised 134 experiments reporting on the responses of 36 small mammal species to the scent of six introduced mesopredators and 12 native mesopredators. For each introduced mesopredator, we measured their phylogenetic and functional distance to local native mesopredators and the number of years sympatric with their prey. We used predator and prey body mass as a measure of predation risk. Globally, small mammals were similarly wary of the scent of native and introduced mesopredators; phylogenetic and functional distance between introduced mesopredators and closest native mesopredators had no effect on wariness; and wariness was unrelated to the number of prey generations, or years, since first contact with introduced mesopredators. Small mammal wariness was associated with predator-prey body mass ratio, regardless of the nativity. The one thing animals do not seem to recognize is whether their predators are native.

KEYWORDS
functional traits, invasion biology, mesopredator, naivety, small mammal

Resumen

La hipótesis de la ingenuidad de la presa plantea que ésta es vulnerable a los depredadores introducidos porque se requiere que muchas generaciones atraviesen una coevolución lenta y gradual para que se desarrollen las respuestas de evasión adecuadas. La hipótesis supone que la presa será más sensible a los depredadores introducidos que difieren notoriamente de los nativos y de aquellos recién establecidos. Realizamos un metaanálisis global de estudios que midieron las respuestas cautelosas de mamíferos pequeños ante el rastro de meso depredadores simpátricos para probar estas suposiciones. Identificamos 26 estudios que cumplieron con nuestro criterio de selección. Estos estudios estuvieron conformados por 134 experimentos que reportaban las respuestas de 36 especies de mamíferos pequeños ante el rastro de seis meso depredadores introducidos y 12 nativos. Medimos la distancia funcional y filogenética entre cada meso depredador introducido y los meso depredadores locales nativos y el número de años simpátricos con su presa. Usamos la masa corporal del depredador y la presa como medida del riesgo de depredación. A nivel mundial, los mamíferos pequeños compartieron la cautela ante el rastro de los meso depredadores nativos e introducidos; la distancia funcional y la filogenética entre los meso depredadores introducidos y el meso depredador nativo más cercano no tuvieron efecto sobre la cautela; y la cautela no estuvo relacionada con el número de generaciones de la presa, o años, desde el primer contacto con los meso depredadores introducidos. La cautela de los mamíferos pequeños estuvo asociada con las proporciones de masa corporal entre el depredador y la presa, sin importar el origen. Lo único que los animales parecen no reconocer es si el depredador es nativo o no.

PALABRAS CLAVE

biología de la invasión, características funcionales, ingenuidad, mamífero pequeño, meso depredador

【摘要】

猎物天真假说认为,猎物容易受到外来捕食者的捕猎,因为它们需要多个世代缓慢的共同进化才能恰当地躲避捕食者。该假说预测猎物对本地捕食者的反应比对外来捕食者的反应更强,且对与本地捕食者和新出现捕食者差异较大的外来捕食者反应更弱。为了检验这些预测,我们对全球小型哺乳动物对同域中型哺乳动物捕食者气味的警戒反应研究进行了荟萃分析。我们确定了 26 项符合筛选标准的研究,包含报告了 36 种小型哺乳动物对 6 种外来中型捕食者和 12 种本地中型捕食者气味反应的 134 项实验。对于每一种外来中型捕食者,我们测量了它们与本地中型捕食者的系统发育距离及功能距离,及其与猎物同域分布的年数。我们还用捕食者和猎物的体重作为捕食风险的衡量标准。结果显示,在全球范围内,小型哺乳动物对本地和外来中型捕食者的气味具有相似的警惕性;外来中型捕食者与最接近的本地中型捕食者之间的系统发育距离及功能距离对警惕性没有影响;且警惕性与猎物和外来中型捕食者首次接触后的世代数或年数无关。小型哺乳动物的警惕性与捕食者-猎物的体重比有关,而与捕食者是否为本地物种无关。由此可见,动物似乎无法分辨捕食者是本地物种还是外来物种。【翻译:胡怡思;审校:聂永刚】

关键词: 入侵生物学,功能性状,中型捕食者,天真,小型哺乳动物

INTRODUCTION

Invasion biology is founded on the idea that slow and gradual reciprocal adaptation is necessary to enable stable species interactions. Introduced species are considered "disruptive" of "co-evolved" ecological communities and processes, that "damage" native species because of their "lack of evolutionary adaptations" to "aliens" (Paolucci et al., 2013). Introduced mammalian mesopredators in particular are regarded as "agents

of extinction" and "the most damaging group of alien animal species for global biodiversity" (Doherty et al., 2016). They are said to "inflict severe impacts" whether their populations are high or low due to the "sensitivity" of native prey (Legge et al., 2017).

There are two main reasons for this dire assessment. First, introduced predators hunt native animals, including threatened species (Bonnaud et al., 2011; Johnson & Isaac, 2009). Second, the introduction, rise, and fall of introduced

mammalian mesopredators correlate in some cases with the fates of native animals they prey on. For example, in Australia, several small mammals declined and went extinct after mesopredator introductions (Johnson, 2006); others persisted where these mesopredators had yet to establish (Legge et al., 2018); and some increased after they were suppressed by conservation killing programs (Hunter et al., 2018). These lines of evidence converge to point toward predation by introduced mammalian mesopredators as a plausible contributor to extinction.

Because predation is foundational to life (Bengtson, 2002) and most animals evolved with a wide range of predators and predatory behaviors, the sweeping claim that animals are unusually vulnerable to introduced predators requires a biological mechanism. It has been proposed that the hunting abilities of introduced mesopredators may be "superior" (Bannister et al., 2018) or that the avoidance skill of native prey may be "inferior" (Garland et al., 1988). Evidence has not emerged that introduced mesopredators are exceptional hunters. It also appears that most native prey are physically capable of escaping introduced predators (Garland et al., 1988), with some notable exceptions (Wright et al., 2016). Instead, the primary avenue of research has focused on the prey's wariness responses to introduced predators. Invasion biology's proposed mechanism for the assertion that introduced predators have greater effects on their prey than native predators, termed the prey naivety hypothesis, is that native prey fail to recognize or respond appropriately to predators with whom they have shared a relatively brief evolutionary history (Anton et al., 2020; Carthey & Banks, 2014; Paolucci et al., 2013). Significant attention has been devoted to testing this hypothesis, starting at least four decades ago and continuing to this day (e.g., Dickman & Doncaster, 1984; Steindler & Letnic, 2021).

The proposition that coevolution, developing over many generations, is needed for prey to respond effectively (i.e., with savviness) to their predators is persuasive. It is founded on the idea of evolution as a gradual and slow process (Carroll et al., 2007). Populations isolated from predators on islands have offered the clearest examples of naivety (Blumstein & Daniel, 2005; Cooper Jr et al. 2014). Charles Darwin famously described the "very silly birds" that were easily approached and hunted on a previously human-free island (Darwin, 1840). Animals raised in captivity show similar vulnerabilities. When released, they are often rapidly hunted by introduced predators (Moseby et al., 2011), but also by native predators (Berger-Tal et al., 2020; Heezik et al., 1999). Wild animals can be similarly unresponsive to predators they have little or no experience with. In North America, moose (*Alces alces*) are less responsive to the sounds and scents of decades-long extinct wolves (*C. lupus*) and brown bears (*Ursus arctos*) and initially more vulnerable to predation when these predators recolonized (Berger et al., 2001). Female elk (*Cervus elaphus*) and bison (*Bison bison*) are less vigilant where wolves have been extinct for decades compared with those in areas where wolves have recolonized (Laundré et al., 2001). It is fair to conclude that short-term naivety to unfamiliar predators, native and not, is well supported and provides a reasonable starting point for considering why animals might be particularly vulnerable to introduced predators. Yet, most

extant animals have been living with introduced predators for generations, attesting to their prowess and that of their ancestors who survived first contact. Invasion biology proposes that heightened vulnerability to introduced predators is persistent despite lived experience and ongoing selection pressure across generations (Anton et al., 2020). This is the claim we sought to address.

Although many traits evolve slowly, others evolve at an ecological pace that enables rapid adaptation to novel organisms (Carroll et al., 2007). Learning and teaching also play important roles in individual and social adaptation (e.g., Thornton & McAuliffe, 2006). There is evidence that this capacity for flexible adaptation and learning occurs in prey responding to introduced predators. In a striking parallel, comparisons of red fox (*Vulpes vulpes*) abundance on either side of the Israel-Jordan border (foxes native) (Shapira et al., 2008) and on either side of the Dingo Barrier Fence (foxes introduced) (Letnic & Dworjanyn, 2011) showed there is less small mammal foraging where foxes are more common. Similarly, a meta-analysis showed that Australian native mammals respond to the cues of introduced predators as strongly as to native predators (Banks et al., 2018). In support of the view that naivety is not immutable, but rather is a function of experience, northern brown bandicoots (*Isoodon macrourus*) are more responsive to the scent of introduced red foxes where the two species are sympatric compared with where they are allopatric (Bytheway & Banks, 2019). The important questions for conservation, however, are whether such rapid adaptation is common or rare and how long it takes to develop.

Inexperienced prey can learn and adapt to new predators rapidly. In central Australia, one group of semicaptive burrowing bettongs (*Bettongia lesueur*) exposed to introduced cats (*Felis silvestris catus*) increased wariness behaviors within 18 months (West et al., 2018); became larger and faster within 4 years (Tay et al., 2021); and were responsive to the scent of cats, unlike inexperienced bettongs (Saxon-Mills et al., 2018). Similarly, predator-inexperienced brushtail possums (*Trichosurus vulpecula*) avoid introduced cat urine 12 months after release (Bannister et al., 2018). These cases parallel observations of prey rapidly learning to respond to native predators that they had been isolated from (e.g., Berger et al., 2001; Cunningham et al., 2019; Laundré et al., 2001; Zidon et al., 2009). Whether inexperienced prey become familiar with native predators more quickly than with introduced predators has not been tested.

Just as naivety can be rapidly overcome with experience, isolation from both native and introduced predators can turn once-savvy prey naïve. Northern quolls (*Dasyurus hallucatus*) isolated from (native) dingoes (*Canis dingo*) and (introduced) cats on an Australian island for 13 years were less responsive to the scent of both predators compared with mainland quolls (Jolly et al., 2018); animal populations in close contact with humans (where some predators are less common) reduce antipredator behaviors within 20 generations on average (Geffroy et al., 2020); Gulf Island raccoons (*Procyon lotor*) lost the fear of cougars extirpated in the 20th century (Suraci et al., 2017); brushtail possums isolated from introduced mammalian predators for 15 years spend more time on the ground

compared with predator-experienced possums (Bannister et al., 2018); and tammar wallabies (*Macropus eugenii*) introduced to New Zealand and isolated from predators for 130 years do not adopt antipredator vigilance behaviors relative to group size, unlike predator-experienced Australian populations (Blumstein et al., 2004).

Because the prey naivety hypothesis is based on the idea that prey responses evolve over many generations, some have logically predicted that prey should be particularly naïve to introduced predators that are phylogenetically or functionally distant from native predators (Anton et al., 2020; Banks et al., 2018; Ehlman et al., 2019; Ricciardi & Atkinson, 2004; Sih et al., 2010). In Australia, Carthey and Banks (2012) found that bandicoots (*Perameles nasuta*) forage less in residential yards that contain dogs (*C. familiaris*) compared with those with cats, an observation they attribute to bandicoot's relative familiarity with dogs, which are closely related to native dingoes. However, they acknowledge that the difference in antipredator behaviors could also reflect differences in predation risk. Similarly, Cremona et al. (2014) found that rock rats (*Zyzomys* spp) are more responsive to northern quolls than to dingoes, which could be attributed to the longer history they share with quolls or to differences in predation risk. In fact, the role of relative predation risk in behavioral responses to introduced compared with native predators has not been assessed. Previous meta-analyses showed limited support for the prey naivety hypothesis (Anton et al., 2020; Banks et al., 2018), possibly due to the mixing of studies involving predator-experienced and inexperienced prey and of low- and high-risk predators.

Due to the importance of the prey naivety hypothesis to invasion biology, we conducted a global meta-analysis of studies focused on predator-experienced animals (small mammals) responding to the cues of high-risk predators (mammalian mesopredators) that have long coevolved with them (native) or were recently introduced to them (introduced). By focusing on this cohort, we were able to test the prey naivety hypothesis where it is most relevant to conservation: predator–prey interactions predicted to lead to extinctions. We tested four key predictions made by the prey naivety hypothesis: prey will be warier of native than introduced predators; prey will be least wary of introduced predators that are phylogenetically and functionally distinct from native predators; prey will be warier of introduced predators they have co-occurred with the longest; and prey wariness will increase as predation risk increases, but only when the predator is native. The prey naivety hypothesis is supported if any one of these predictions is met.

METHODS

We conducted a literature search for predation risk experiments in Google Scholar, Web of Science, and Scopus with combinations of the search terms "*naivety*" and "*predator*," for the prey naivety hypothesis; "*giving up density*," for a method commonly used to assess prey perception of predation risk (Verdolin, 2006); "*scent*," for a predator cue that is species-specific and commonly used (Carthey & Banks, 2014); and "*Vulpes*," "*Felis*,"

"*Mustela*," and "*Herpestes*," for introduced mesopredators considered most likely to cause extinctions (Doherty et al., 2016). We also searched through the literature lists of, and citations to, relevant studies. Detailed search methods are in Appendix S1.

To focus on predator–prey interactions most strongly associated with extinctions and to reduce confounding variables, we filtered the selection to studies of small mammals (<5 kg) responding to the scent of a larger mammalian mesopredator (1–14 kg). We chose these body mass ranges to focus on high-risk predation (i.e., prey responding to their main predators) (Cohen et al., 1993; Cruz & Pires, 2022; Tucker & Rogers, 2014). To test for naivety in populations of predator-experienced animals, we filtered the studies further to include only experiments conducted under free-ranging conditions, where the predator was sympatric, and on animals that had been born locally (or had immigrated independently). We, therefore, excluded studies conducted in labs, enclosures, exclosures, and human dwellings and studies of captive-born or translocated animals. Finally, we excluded studies examining small mammal responses to native mesopredators introduced to a region where the predator and prey were previously allopatric (e.g., native mesopredator introduced to the offshore island) because these relationships do not fit into a native or introduced category unambiguously. Studies were also included only if the necessary data could be extracted (mean, a measure of variance, and sample size). Data collection ended in January 2022. Details on the literature filtering and selection process are in Appendix S1.

The final data set included 26 studies composed of 134 experiments (Appendix S2). These studies reported on the responses of 36 small mammal species (~10–2000 g) to the scent of six introduced mesopredators (one canid, one felid, two dasyurids, and two mustelids) and 12 native mesopredators (five canids, two felids, two dasyurids, two mustelids, and one euplerid). No experiments involving other cue types other than scent (e.g., sound) were found. The studies were geographically widespread (all continents other than Antarctica). Most studies of introduced pairs were conducted in Australia (nine studies); studies of native pairs were more equally distributed (top 3: six in Australia, six in North America, and four in Europe) (Appendix S3). The search was conducted only in English, and only publications in English were found.

All experiments compared small mammal wariness responses to the scent of a mesopredator compared with a control scent. Weaker wariness responses of prey to introduced predators compared with native predators was interpreted as evidence of long-term naivety (Carthey & Banks, 2014). Overall, the selected studies used four experiment types—giving up density, trapping, flight initiation distance, and activity—that measured four main responses by small mammals to mesopredator scent relative to a control: foraging, wariness behaviors, activity rates, and stress hormones. We included all behavior data that were clearly defined by the study authors as wariness responses (e.g., vigilance) and excluded behavior data that were not defined as wariness (e.g., walking). Predator scents applied were scats, urine, and the whole body. The controls were odorless, herbivore scent, or a novel chemical scent. Some studies included more than one control type; in which case, we chose the

odorless control. We excluded comparisons with the scent of the small mammal being tested because this scent can act as an attractant.

To test whether prey are warier of native compared with introduced predators, we categorized the relationship between the small mammal and mesopredator as either native or introduced based on whether they co-occurred before the onset of humanity's last major global expansion (~500 years ago). Predator–prey pairs that were locally introduced but sympatric in their native range were considered native pairs (e.g., European rabbit [*Oryctolagus cuniculus*] and red fox in Australia). In the final data set, all introduced predator–prey pairs in the selected studies shared <200 years of sympatry.

To test whether small mammals were least wary of introduced predators that differed substantially from their native predators, we first identified all native mammalian mesopredators that overlapped with each prey. Given the range contraction of some mesopredators, we used PHYLACINE 1.2, which estimates distributions in the absence of historic and prehistoric extirpations (Faurby & Svenning, 2015). We then analyzed small mammal wariness responses to the scent of introduced mesopredators relative to phylogenetic and functional distance from the most similar native mesopredator.

We used the phylogeny provided by PHYLACINE 1.2 and the function cophenetic.phylo in the R package ape (Paradis & Schliep, 2019) to calculate the phylogenetic distance between each introduced mesopredator and all overlapping native mesopredators. We then used the closest phylogenetic distance with a native mesopredator as the predictor of prey wariness.

To quantify functional distance, we first compiled a data set of functional traits of each introduced mesopredator and all overlapping native mesopredators. We selected six predator traits that we considered of particular relevance to prey: body mass, diet, hunting habitat, daily activity patterns, hunting locomotion, and cooperative hunting (Appendix S4). Predator body mass and diet (percent vertebrate, invertebrate, and plant) influence prey selection and hunting pressure; hunting habitat (terrestrial, arboreal, and fossorial) and daily activity patterns (crepuscular, diurnal, and nocturnal) determine spatiotemporal overlap with prey; and evading predators requires adaptation to differences in hunting styles (locomotion, e.g., ambush vs. cursorial and cooperative vs. solitary). We then used these functional traits to calculate the Gower distance between introduced mesopredators and the overlapping native mesopredators with the R package FD (Laliberté et al., 2014). Gower distance is a flexible distance-based metric that can handle mixed data types and describes the overall pairwise functional dissimilarity between species. We then used the closest Gower distance with a native mesopredator as the predictor of prey wariness.

To test the prediction that prey will be warier of longer-established introduced predators, we analyzed wariness to introduced mesopredator scent relative to the number of years and the number of small mammal generations since first contact. The number of years since first contact was calculated from the estimated year the introduced mesopredator established in the study site to the year the study was conducted, or

if not stated, to the year the study was submitted to the publishing journal. The number of small mammal generations shared with introduced mesopredators was calculated by dividing the number of years since first contact by the small mammal's estimated generation length. Generation length has several definitions and methods of calculation. We relied on Pacifici et al. (2013), who calculated generation length for all mammals with the International Union for the Conservation of Nature Red List Guidelines' equation, which incorporates age at first reproduction with reproductive lifespan accounting for estimates of survivorship and fecundity over time. For mammals without detailed life-history data, Pacifici et al. (2013) made assessments, for example, based on the life history of congenerics.

To test the prediction that prey wariness increases with predation risk—only when the predator is native—we determined whether small mammal wariness to mesopredator scent varied according to small mammal body mass (Appendix S3) and according to the ratio of small mammal body mass to mesopredator body mass (Appendix S4). We used body mass metrics because they are fundamental predictors of predation risk and because information on local predation rates was not available. Within terrestrial mammals, larger predators tend to hunt larger prey (Cohen et al., 1993; Tucker & Rogers, 2014). Among Neotropical Carnivora, the relationship between predation rate and predator-prey body mass ratios follows a bell-shaped curve, and prey <5% of the predator's body mass are most often hunted (Cruz & Pires, 2022). To determine whether small mammals were more responsive to variations in predation risk by native mesopredators, we compared the wariness of predator scent relative with these predation risk metrics (prey body mass and predator-prey body mass ratio) between native and introduced mesopredators.

We extracted the mean and error of treatment and control with ImageJ and calculated the effect size of small mammal wariness. We used Hedges' *g* (Equation 1), a valueless measure that describes differences between control and treatments within a study, standardized by study sample size and variance. Hedges' *g* can accept negative values unlike other commonly used effect size estimators (e.g., a log-transformed ratio of means). Hedges' *g* was calculated in R package (4.0.3) metafor (2.4-0) after converting all measures of the error to standard deviation. The results from each study and experiment are in Appendix S2. Typically, Hedges' *g* effect values are considered small at ~0.2, medium at ~0.5, and large at ~0.8 (Cohen, 1992).

$$ g = \frac{M_{\text{predator}} - M_{\text{control}}}{\sqrt{\frac{(n_{\text{predator}} - 1) \times \text{SD}_{\text{predator}}^2 + (n_{\text{control}} - 1) \times \text{SD}_{\text{control}}^2}{(n_{\text{predator}} + n_{\text{control}} - 2)}}}, \quad (1) $$

where M is the group mean, n is the sample size, and SD is the standard deviation for each experimental treatment (mesopredator scent vs. control scent).

We then constructed successive meta-regression models to test each hypothesis with the function rma.mv in the R package metafor. These models weight the influence of each data

point by the inverse of the sampling variance and the amount of heterogeneity captured by random effects (Viechtbauer, 2010), thus accounting for discrepancies in study strength. Given the large number of potential random effects that could influence the results, we formulated 24 biologically defensible random error structures. These included different nested and crossed combinations of the reference identification, prey and predator species, study site, continent, and the climate zone of the study site (Köppen-Geiger zones, from Beck et al. [2018]). We then used a cross-validation approach to select the best random effect structure for each model. We did this by randomly resampling 70% of the data set over 1000 iterations per potential random effect structure. On each iteration, we compared the predicted effect sizes for the remaining 30% of data with the observed effect sizes and calculated the absolute deviation between predicted and observed values (how inaccurate the model predictions were). We selected the model with the least mean absolute deviation after excluding models with random error sigmas (variance) of 0, indicating overfitting and convergence problems. Final model specifications are in Appendix S5; cross-validation results are in Appendix S6; and data and custom scripts are available on Figshar https://doi.org/10.6084/m9.figshare.21194971.

RESULTS

Small mammal wariness response strength to the scent of both native and introduced mesopredators was medium to large (introduced: Hedges' $g = 0.6$, 95% confidence interval [CI] 0.3−0.9, $p = 0.0006$; native: $g = 0.6$, 95% CI 0.3−0.9, $p < 0.0001$) (Figure 1 & Appendix S5). There was no difference in response based on nativity ($p = 0.81$). The strength of wariness responses to introduced mesopredator scent was unaffected by phylogenetic or functional distance from the most similar native mammalian mesopredator (phylogenetic distance: coefficient = 0.3, 95% CI −0.6 to 1.2, $p = 0.49$; functional distance: coefficient = 1.3, 95% CI −0.9 to 3.4, $p = 0.25$) (Figure 2 & Appendix S5). Wariness was also unrelated to the number of years (coefficient = 0.002, 95% CI −0.01 to 0.01, $p = 0.7$) (Appendix S5) or the number of small mammal generations (coefficient = 0.003, 95% CI −0.008 to 0.014, $p = 0.62$) (Figure 3 & Appendix S5) since the estimated year of first contact with introduced mesopredators.

Wariness responses to native and introduced mesopredator scent were positively correlated with small mammal body mass (coefficient = 0.54, 95% CI 0.2−0.9, $p = 0.001$) and with predator-prey body mass ratio (coefficient = 0.43, 95% CI = 0.1−0.7, $p = 0.008$) (Figure 4 & Appendix S5). This relationship was similar for both introduced and native small mammals ($p = 0.39−0.43$) (Figure 4 & Appendix S5).

DISCUSSION

We tested the prey naivety hypothesis where it matters most to conservation: the responses of predator-experienced prey to introduced predators attributed with causing extinctions. We found that small mammals were wary of mesopredator scent regardless of nativity and of how phylogenetically and functionally distant introduced mammalian mesopredators were from native mammalian mesopredators; naivety was undetectable in the wild within the shortest period research had documented; and small mammals were responsive to (a metric of) predation risk posed by introduced and native mesopredators alike. Invasion biology's fundamental claim that long-term coevolution is necessary for prey to recognize their predators is, therefore, unsupported by available evidence.

Our findings reinforce the results of the meta-analysis by Banks et al. (2018) that Australian small mammals respond with equal wariness to native and introduced predators and by Anton et al. (2020), who found no evidence of naivety in terrestrial animals globally. However, our results contrast with the conclusion of Anton et al. (2020) that prey are naive to introduced predators which are phylogenetically distinct from native predators. They found higher prey wariness in response to introduced predators in the same genus as a local native predator. That we found no effect of phylogenetic or functional distance of introduced mesopredators from native mesopredators on small mammal wariness suggests that prey do not consider introduced predators aliens. Our results also depart from the conclusion of Anton et al. (2020) that it should take ∼200 generations to "erode naiveté." We found no effect of the number of prey generations, or of years since first contact, on wariness toward the introduced mesopredator scent, suggesting that learning and adaptation occurred before the research was conducted. One reason for the differences between our findings and that of previous studies is the inclusion criteria. Previous analyses merged studies of predator-inexperienced and -experienced prey, low- and high-risk predators, sympatric and allopatric predators, and a range of taxonomic groups. We focused on studies most likely to reveal responses of locally born, predator-experienced prey to high-risk predators in defined taxonomic groups.

Predator-savvy prey are, by definition, responsive to predation risk. We were not able to test wariness as a function of predation rate because the studies did not report this information. However, body mass showed a strong explanatory signal. Strikingly, the association between wariness and body mass was similar between native and introduced predator–prey pairs, suggesting that what prey recognize is not whether their predator is native but to what extent their predator is a risk. Specifically, we found that larger small mammals were warier of mesopredator scent. It is plausible that in these trophic groups larger prey are warier of mesopredator scent because their risk of predation is higher. Our results align with a study of flight initiation distance in birds. Blumstein (2006) found that larger birds are warier of humans. Predation risk varies with predator and prey body masses among native species (Cohen et al., 1993; Cruz & Pires, 2022; Tucker & Rogers, 2014), as it does among introduced predators and prey. In Australia, it has been suggested that the relative probability of predation by introduced red foxes and cats on nonflying native mammals increases up to ∼1 kg (Stobo-Wilson et al., 2021) and for cats peaks at 0.5 kg (Woolley et al.,
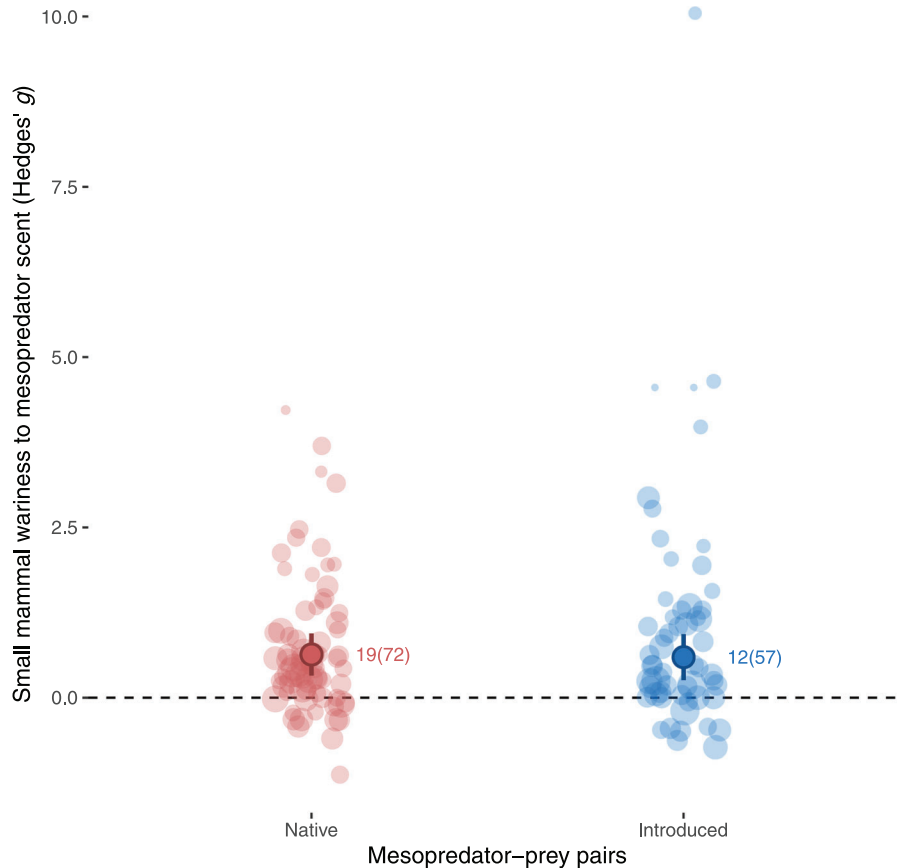
FIGURE 1   Wariness response of small mammals to the scent of introduced and native mesopredators (light shading, individual experiment effect sizes; circle size, proportional to data weight in the analyses; dark shading, model estimates of the overall effect of predator scent on native and introduced wariness responses across studies; error bars, 95% confidence intervals; colored numbers, number of studies and in parentheses number of experiments). Sampling variance is determined by sample size and error. Native and introduced species are categorized based on the relationship between the prey and the predator being tested, rather than the species' relationship to the study site. Excluding the outlier point among introduced pairs did not influence results (introduced wariness without outlier: estimate = 0.64, z = 4.0, p < 0.0001 vs. with outlier: estimate = 0.65, z = 4.0, p < 0.0001).

2019), which is within the range of body masses we tested for. To our knowledge, naivety experiments have not considered the effects of body mass or other functional or life history traits on responsiveness to introduced predators. Our body mass results lend support to the methodological rigor of the reviewed studies. The association between wariness and body mass was strong despite the noise one would expect from wariness data derived from an indirect cue of risk (predator scent), across a range of species and ecosystems, and with wariness interpreted with a range of behavioral metrics.

The prey naivety hypothesis is not only important to understanding the effects of introduced predators, but also foundational to invasion biology, which asserts that introduced species remain non-native in their new homes even after multiple generations (Davis, 2009). If the prey can adapt to introduced predators, it seems likely that other types of species interactions are at least as flexible and adaptive. Indeed, plants enhance defenses to introduced herbivores (Bailey et al., 2007); rapid adaptation, including learning, occurs in predators hunting precarious introduced prey with surprisingly toxic glands (Shine, 2010); introduced species are pulled back into the food chain

as native species adapt to consume them (Carroll et al., 2005; Lundgren et al., 2022); and new competitors find ways to coexist (Malo et al., 2016; Reus et al., 2014).

Although we can confirm that populations that survive first contact are typically savvy, there is one important limitation to this conclusion: most studies conducted in the wild focused on nonthreatened species. The available research, however, does not show that threatened species are less savvy about introduced predators. In their meta-analysis, Banks et al. (2018) found that threatened and nonthreatened Australian mammals are equally responsive to introduced predators, although their sample size was low. Our literature search identified only one study of a threatened species that fit our inclusion criteria: Steindler and Letnic (2021) found that bilbies (*Macrotis lagotis*, vulnerable) respond to the scent of introduced cats. The effect size of this response was within the range of studies of non-threatened small mammals (Appendix S2). Similarly, studies of dusky hopping mouse (*Notomys fuscus*, vulnerable) predation responses reinforce the notion that threatened mammals are wary of introduced mesopredators (Gordon et al., 2015; Letnic & Dworjanyn, 2011) (not included in our analysis). Naivety
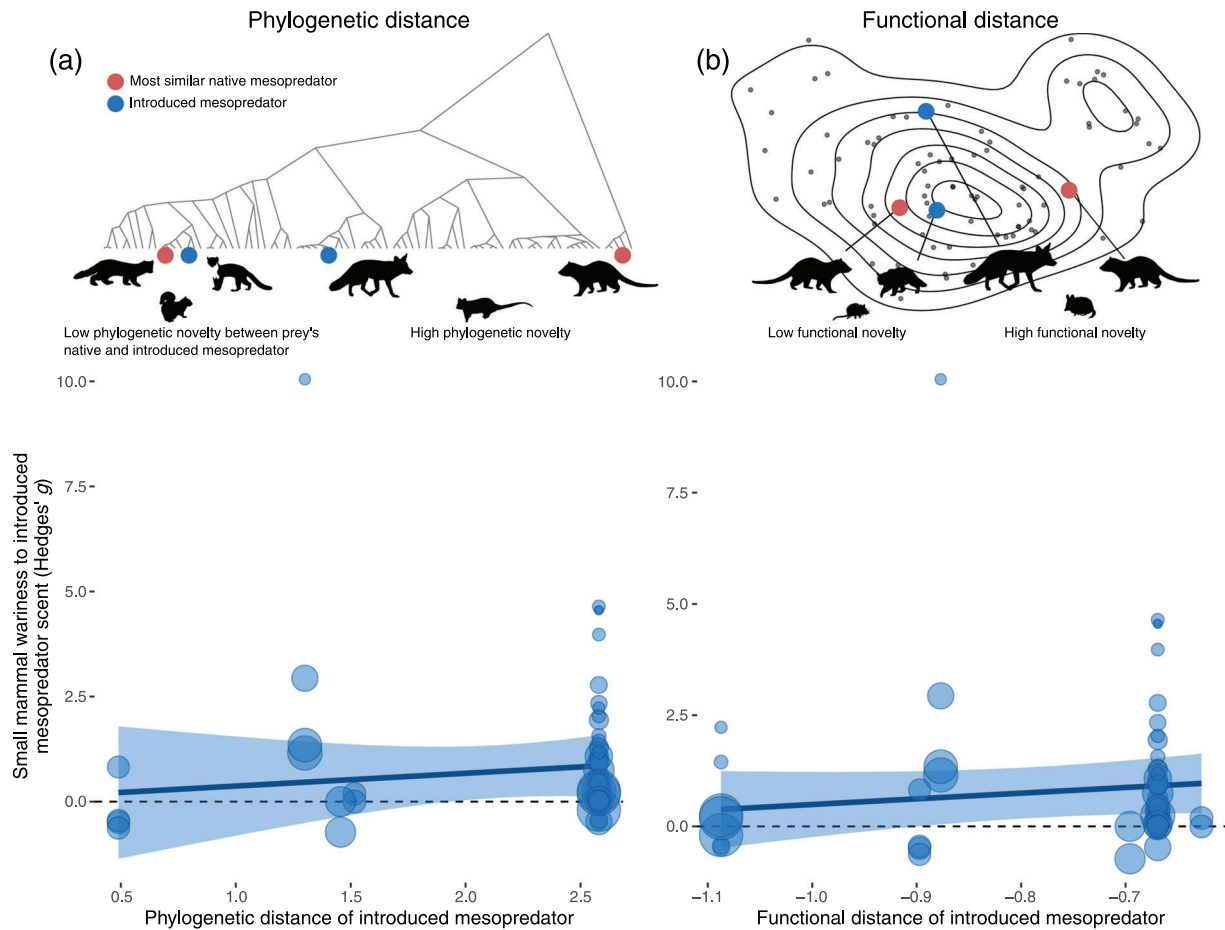
FIGURE 2 Effects of (a) phylogenetic distance and (b) functional distance to closest native mesopredators on small mammal wariness to the scent of introduced mesopredators (circles, individual experiments; circle size, proportional to data point weight in the analyses; regression line, model estimates and confidence intervals). Sampling variance is determined by sample size and variance. Some studies include several experiments. Upper panels provide examples of high and low novelty (i.e., long and short phylogenic and functional distances).

may play a role in the vulnerability of predator-inexperienced animals, such as those isolated in captivity, on off-shore islands, and in fenced reserves. This has given rise to attempts to train captive animals to recognize predators they are likely to encounter when released (e.g., native: Heezik et al. [1999]; e.g., introduced: Moseby et al. [2012]).

It is possible, however, that naivety contributed to past extinctions (Blackburn et al., 2004). Although this is of course untestable and irrevocable, it does have some implications for conservation. Based on our results, we cannot predict whether a future predator introduction would result in prey extinction. In fact, our review of the literature suggests that both reintroductions (of native predators) and introductions (of non-native predators) can result in heightened predation pressure on inexperienced prey. Any introduction or reintroduction is thus likely to increase the rate of death and injury to prey, at least for a time, which could lead to extirpation or even global extinction if their population is small. However, prey that survive first contact to subsequently co-occur with introduced predators for several generations, or even just for a few years, should be savvy.

Animals long thought of as "notably less intelligent" and relatively "simple" (Britannica, 2021) have turned out to be smart (Todorov et al., 2021), fast (Garland et al., 1988), and savvy (this study). Where does this leave the notion that introduced species, particularly predators, are a categorical threat? Our study does not test the claim that introduced predators might have stronger suppressive effects on their prey compared with native predators. An effect can be correctly described, while the underlying mechanism remains unknown. However, that decades of research has not yielded evidence for a mechanism lends support to an alternative view: the native and introduced categories are artificial constructs (Chew & Hamilton, 2011). Without an understanding of what makes introduced species a distinct class, one might be liberated to ask whether they are, in fact, a distinct class (Pereyra, 2020). It is, for example, plausible that suppressive effects attributed to introduced predators can be ecologically contextual rather than evolutionarily predetermined (Didham et al., 2005; Doherty et al., 2015; Wallach et al., 2015). If animals do not distinguish between native and introduced species, perhaps conservationists can let go of this distinction as well.
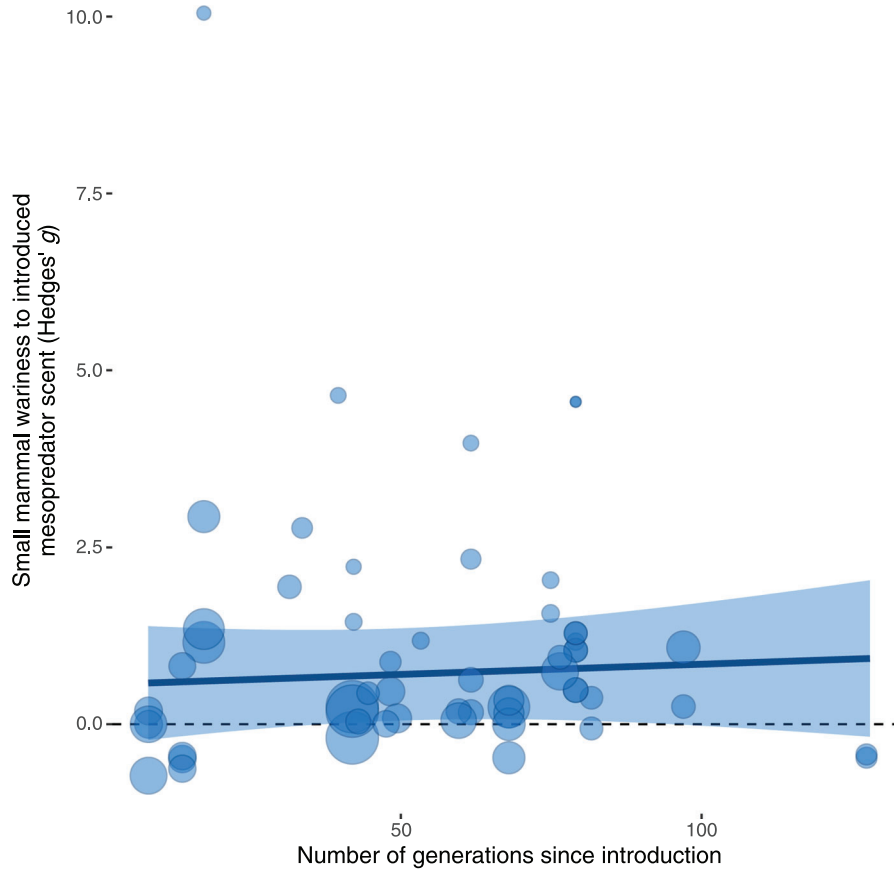
FIGURE 3 Association between small mammal wariness to the scent of introduced mesopredators and the number of prey generations since first contact with introduced mesopredators (circles, individual experiments; circle size, proportional to data point weight in the analyses, e.g., sampling variance determined by sample size and error; regression lines, model estimates and confidence intervals). The number of generations is based on generation lengths calculated by Pacifici et al. (2013). Some studies include several experiments.
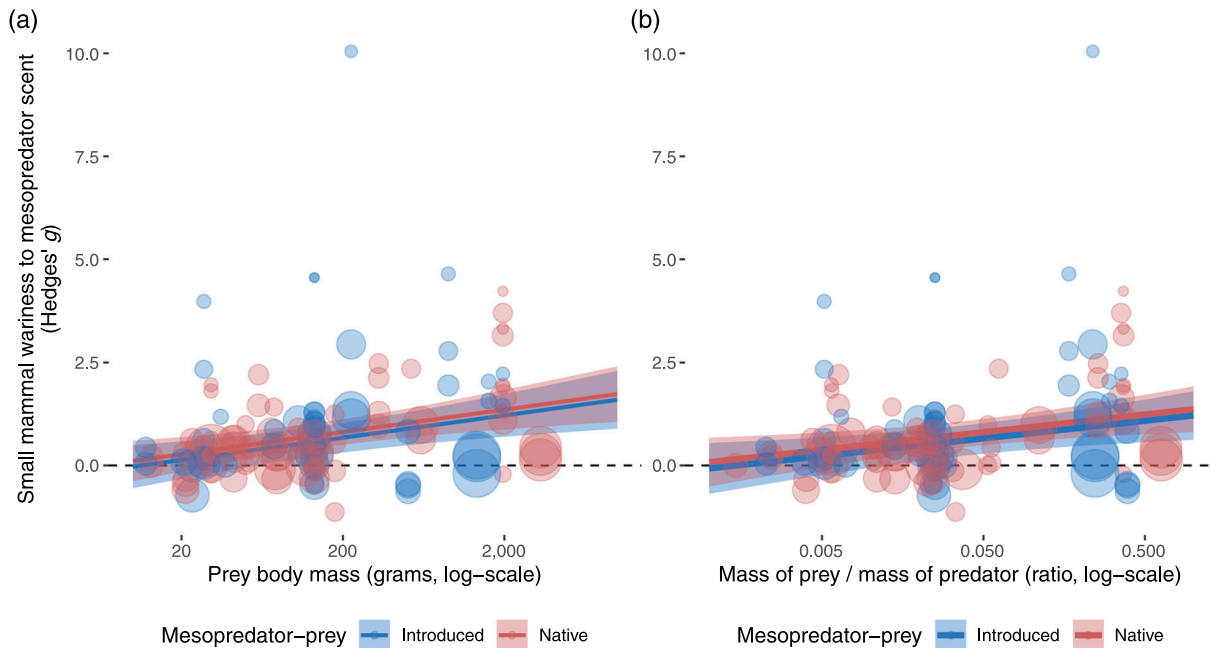
FIGURE 4 Effects of (a) prey body mass and (b) ratio of prey mass to predator mass on small mammal wariness to the scent of introduced and native mesopredators (circles, individual experiments; circle size, data weight in the analyses; regression lines, model estimates and confidence intervals). Sampling variance is determined by sample size and error. Native and introduced are categorized based on the relationship between the prey and the predator being tested, rather than the species' relationship to the study site. Some studies include several experiments.

ORCID

Arian D. Wallach https://orcid.org/0000-0002-6640-3887
Ana Benítez-López https://orcid.org/0000-0002-6432-1837

REFERENCES

Anton, A., Geraldi, N. R., Ricciardi, A., & Dick, J. T. (2020). Global determinants of prey naiveté to exotic predators. *Proceedings of the Royal Society B*, *287*, 20192978.

Bailey, J. K., Schweitzer, J. A., Rehill, B. J., Irschick, D. J., Whitham, T. G., & Lindroth, R. L. (2007). Rapid shifts in the chemical composition of aspen forests: An introduced herbivore as an agent of natural selection. *Biological Invasions*, *9*, 715–722.

Banks, P. B., Carthey, A. J., & Bytheway, J. P. (2018). Australian native mammals recognize and respond to alien predators: A meta-analysis. *Proceedings of the Royal Society B*, *285*, 20180857.

Bannister, H., Brandle, R., & Moseby, K. (2018). Antipredator behaviour of a native marsupial is relaxed when mammalian predators are excluded. *Wildlife Research*, *45*, 726–736.

Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, *5*, 180214.

Bengtson, S. (2002). Origins and early evolution of predation. *Paleontological Society Papers*, *8*, 289–318.

Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naive prey: Conservation lessons from pleistocene extinctions. *Science*, *291*, 1036–1039.

Berger-Tal, O., Blumstein, D., & Swaisgood, R. R. (2020). Conservation translocations: A review of common difficulties and promising directions. *Animal Conservation*, *23*, 121–131.

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., & Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science*, *305*, 1955–1958.

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: How life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, *71*, 389–399.

Blumstein, D. T., & Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 1663–1668.

Blumstein, D. T., Daniel, J. C., & Springett, B. P. (2004). A test of the multipredator hypothesis: Rapid loss of antipredator behavior after 130 years of isolation. *Ethology*, *110*, 919–934.

Bonnaud, E., Medina, F. M., Vidal, E., Nogales, M., Tershy, B., Zavaleta, E., Donlan, C., Keitt, B., Le Corre, M., & Horwath, S. (2011). The diet of feral cats on islands: A review and a call for more studies. *Biological Invasions*, *13*, 581–603.

Britannica. (2021). The Editors of Encyclopaedia. "marsupial". Encyclopedia Britannica. https://www.britannica.com/animal/marsupial

Bytheway, J. P., & Banks, P. B. (2019). Overcoming prey naiveté: Free-living marsupials develop recognition and effective behavioral responses to alien predators in Australia. *Global Change Biology*, *25*, 1685–1695.

Carroll, S. P., Hendry, A. P., Reznick, D. N., & Fox, C. W. (2007). Evolution on ecological time-scales. *Functional Ecology*, *21*, 387–393.

Carroll, S. P., Loye, J. E., Dingle, H., Mathieson, M., Famula, T. R., & Zalucki, M. P. (2005). And the beak shall inherit - Evolution in response to invasion. *Ecology Letters*, *8*, 944–951.

Carthey, A. J., & Banks, P. B. (2012). When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. *PLoS ONE*, *7*, e31804.

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, *89*, 932–949.

Chew, M. K., & Hamilton, A. L. (2011). The rise and fall of biotic nativeness: A historical perspective. In D. M. Richardson (Ed.). *Fifty years of invasion ecology: The legacy of Charles Elton* (pp. 35–48). Wiley-Blackwell.

Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*, 155.

Cohen, J. E., Pimm, S. L., Yodzis, P., & Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, *62*, 67–78.

Cooper, W. E., Jr, Pyron, R. A., & Garland, Jr T. (2014). Island tameness: Living on islands reduces flight initiation distance. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20133019.

Cremona, T., Crowther, M. S., & Webb, J. K. (2014). Variation of prey responses to cues from a mesopredator and an apex predator. *Austral Ecology*, *39*, 749–754.

Cruz, L. R., & Pires, M. M. (2022). Body mass ratios determine dietary patterns and help predicting predator–prey interactions of neotropical carnivora. *Mammal Research*, *67*, 1–9.

Cunningham, C. X., Johnson, C. N., Hollings, T., Kreger, K., & Jones, M. E. (2019). Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species. *Ecography*, *42*, 2053–2059.

Darwin, C. (1840). *Journal of researches into the geology and natural history of the various countries visited by HMS Beagle under the command of Captain Fitzroy, RN from 1832 to 1836*. London: Henry Colburn.

Davis, M. A. (2009). *Invasion biology*. Oxford University Press.

Dickman, C., & Doncaster, C. (1984). Responses of small mammals to red fox (*Vulpes vulpes*) odour. *Journal of Zoology*, *204*, 521–531.

Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., & Gemmell, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, *20*, 470–474.

Doherty, T. S., Dickman, C. R., Nimmo, D. G., & Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation*, *190*, 60–68.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*, 11261–11265.

Ehlman, S. M., Trimmer, P. C., & Sih, A. (2019). Prey responses to exotic predators: Effects of old risks and new cues. *American Naturalist*, *193*, 575–587.

Faurby, S., & Svenning, J. C. (2015). Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, *21*, 1155–1166.

Garland, J.-T., Geiser, F., & Baudinette, R. (1988). Comparative locomotor performance of marsupial and placental mammals. *Journal of Zoology*, *215*, 505–522.

Geffroy, B., Sadoul, B., Putman, B. J., Berger-Tal, O., Garamszegi, L. Z., Møller, A. P., & Blumstein, D. T. (2020). Evolutionary dynamics in the Anthropocene: Life history and intensity of human contact shape antipredator responses. *PLoS Biology*, *18*, e3000818.

Gordon, C. E., Feit, A., Grüber, J., & Letnic, M. (2015). Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142870.

Heezik, Y. V., Seddon, P. J., & Maloney, R. F. (1999). Helping reintroduced houbara bustards avoid predation: Effective anti-predator training and the predictive value of pre-release behaviour. *Animal Conservation*, *2*, 155–163.

Hunter, D. O., Lagisz, M., Leo, V., Nakagawa, S., & Letnic, M. (2018). Not all predators are equal: A continent-scale analysis of the effects of predator control on Australian mammals. *Mammal Review*, 48, 108–122.

Johnson, C. (2006). *Australia's mammal extinctions: A 50000 year history*. Cambridge University Press.

Johnson, C. N., & Isaac, J. L. (2009). Body mass and extinction risk in Australian marsupials: The 'Critical weight range'revisited. *Austral Ecology*, 34, 35–40.

Jolly, C. J., Webb, J. K., & Phillips, B. L. (2018). The perils of paradise: An endangered species conserved on an island loses antipredator behaviours within 13 generations. *Biology Letters*, 14, 20180222.

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79, 1401–1409.

Legge, S., Murphy, B., McGregor, H., Woinarski, J., Augusteyn, J., Ballard, G., Baseler, M., Buckmaster, T., Dickman, C., & Doherty, T. (2017). Enumerating a continental-scale threat: How many feral cats are in Australia? *Biological Conservation*, 206, 293–303.

Legge, S., Woinarski, J. C., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., Mitchell, N., Bode, M., Wintle, B., & Baseler, M. (2018). Havens for threatened Australian mammals: The contributions of fenced areas and off-shore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, 45, 627–644.

Letnic, M., & Dworjanyn, S. A. (2011). Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography*, 34, 827–835.

Lundgren, E. J., Ramp, D., Middleton, O. S., Wooster, E. I., Kusch, E., Balisi, M., Ripple, W. J., Hasselerharm, C. D., Sanchez, J. N., & Mills, M. (2022). A novel trophic cascade between cougars and feral donkeys shapes desert wetlands. *Journal of Animal Ecology*, https://doi.org/10.1111/1365-2656.13766

Malo, J. E., González, B. A., Mata, C., Vielma, A., Donoso, D. S., Fuentes, N., & Estades, C. F. (2016). Low habitat overlap at landscape scale between wild camelids and feral donkeys in the Chilean desert. *Acta Oecologica*, 70, 1–9.

Moseby, K. E., Cameron, A., & Crisp, H. A. (2012). Can predator avoidance training improve reintroduction outcomes for the greater bilby in arid Australia? *Animal Behaviour*, 83, 1011–1021.

Moseby, K. E., Read, J. L., Paton, D. C., Copley, P., Hill, B. M., & Crisp, H. A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation*, 144, 2863–2872.

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Marasini, G. G., Visconti, P., & Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, 5, 89.

Paolucci, E. M., MacIsaac, H. J., & Ricciardi, A. (2013). Origin matters: Alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions*, 19, 988–995.

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Pereyra, P. J. (2020). Rethinking the native range concept. *Conservation Biology*, 34, 373–377.

Reus, M. L., Cappa, F. M., Andino, N., Campos, V. E., de Los Rios, C., & Campos, C. M. (2014). Trophic interactions between the native guanaco (*Lama guanicoe*) and the exotic donkey (*Equus asinus*) in the hyper-arid Monte desert (Ischigualasto Park, Argentina). *Studies on Neotropical Fauna and Environment*, 49, 159–168.

Ricciardi, A., & Atkinson, S. K. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, 7, 781–784.

Saxon-Mills, E. C., Moseby, K., Blumstein, D. T., & Letnic, M. (2018). Prey naïveté and the anti-predator responses of a vulnerable marsupial prey to known and novel predators. *Behavioral Ecology and Sociobiology*, 72, 1–10.

Shapira, I., Sultan, H., & Shanas, U. (2008). Agricultural farming alters predator–prey interactions in nearby natural habitats. *Animal Conservation*, 11, 1–8.

Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Quarterly Review of Biology*, 85, 253–291.

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., Preisser, E., Rehage, J. S., & Vonesh, J. R. (2010). Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos*, 119, 610–621.

Steindler, L., & Letnic, M. (2021). Not so naïve: Endangered mammal responds to olfactory cues of an introduced predator after less than 150 years of coexistence. *Behavioral Ecology and Sociobiology*, 75, 1–10.

Stobo-Wilson, A. M., Murphy, B. P., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T. S., Fleming, P. A., Gentle, M. N., Legge, S. M., & Newsome, T. M. (2021). Sharing meals: Predation on Australian mammals by the introduced European red fox compounds and complements predation by feral cats. *Biological Conservation*, 261, 109284.

Suraci, J. P., Roberts, D. J., Clinchy, M., & Zanette, L. Y. (2017). Fearlessness towards extirpated large carnivores may exacerbate the impacts of naïve mesocarnivores. *Behavioral Ecology*, 28, 439–447.

Tay, N. E., Fleming, P. A., Warburton, N. M., & Moseby, K. E. (2021). Predator exposure enhances the escape behaviour of a small marsupial, the burrowing bettong. *Animal Behaviour*, 175, 45–56.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, 313, 227–229.

Todorov, O. S., Blomberg, S. P., Goswami, A., Sears, K., Drhlík, P., Peters, J., & Weisbecker, V. (2021). Testing hypotheses of marsupial brain size variation using phylogenetic multiple imputations and a Bayesian comparative framework. *Proceedings of the Royal Society B*, 288, 20210394.

Tucker, M. A., & Rogers, T. L. (2014). Examining the prey mass of terrestrial and aquatic carnivorous mammals: Minimum, maximum and range. *PLoS ONE*, 9, e106402.

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, 60, 457–464.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Wallach, A. D., Ripple, W. J., & Carroll, S. P. (2015). Novel trophic cascades: Apex predators enable coexistence. *Trends in Ecology & Evolution*, 30, 146–153.

West, R., Letnic, M., Blumstein, D. T., & Moseby, K. E. (2018). Predator exposure improves anti-predator responses in a threatened mammal. *Journal of Applied Ecology*, 55, 147–156.

Woolley, L. A., Geyle, H. M., Murphy, B. P., Legge, S. M., Palmer, R., Dickman, C. R., Augusteyn, J., Comer, S., Doherty, T. S., & Eager, C. (2019). Introduced cats felis catus eating a continental fauna: Inventory and traits of Australian mammal species killed. *Mammal Review*, 49, 354–368.

Wright, N. A., Steadman, D. W., & Witt, C. C. (2016). Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences*, 113, 4765–4770.

Zidon, R., Saltz, D., Shore, L. S., & Motro, U. (2009). Behavioral changes, stress, and survival following reintroduction of Persian fallow deer from two breeding facilities. *Conservation Biology*, 23, 1026–1035.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.