

Trophic cascade driven by behavioral fine-tuning as naïve prey rapidly adjust to a novel predator

CHRIS J. JOLLY ^{1,5}, ADAM S. SMART ¹, JOHN MOREEN,² JONATHAN K. WEBB ³,
 GRAEME R. GILLESPIE,^{1,4} AND BEN L. PHILLIPS ¹

¹School of BioSciences, University of Melbourne, Parkville, Victoria 3010 Australia

²Kenbi Rangers, Mandorah, Northern Territory 0822 Australia

³School of Life Sciences, University of Technology Sydney, Broadway, Ultimo, New South Wales 2007 Australia

⁴Flora and Fauna Division, Department of Environment and Natural Resources, Northern Territory Government, Berrimah, Northern Territory 0828 Australia

Citation: Jolly, C. J., A. S. Smart, J. Moreen, J. K. Webb, G. R. Gillespie, and B. L. Phillips. 2021. Trophic cascade driven by behavioral fine-tuning as naïve prey rapidly adjust to a novel predator. *Ecology* 102(7): e03363. 10.1002/ecy.3363

Abstract. The arrival of novel predators can trigger trophic cascades driven by shifts in prey numbers. Predators also elicit behavioral change in prey populations, via phenotypic plasticity and/or rapid evolution, and such changes may also contribute to trophic cascades. Here, we document rapid demographic and behavioral changes in populations of a prey species (grassland melomys *Melomys burtoni*, a granivorous rodent) following the introduction of a novel marsupial predator (northern quoll *Dasyurus hallucatus*). Within months of quolls appearing, populations of melomys exhibited reduced survival and population declines relative to control populations. Quoll-invaded populations were also significantly shyer than nearby, quoll-free populations of conspecifics. This rapid but generalized response to a novel threat was replaced over the following 2 yr with more threat-specific antipredator behaviors (i.e., predator-scent aversion). Predator-exposed populations, however, remained more neophobic than predator-free populations throughout the study. These behavioral responses manifested rapidly in changed rates of seed predation by melomys across treatments. Quoll-invaded melomys populations exhibited lower per-capita seed take rates, and rapidly developed an avoidance of seeds associated with quoll scent, with discrimination playing out over a spatial scale of tens of meters. Presumably the significant and novel predation pressure induced by quolls drove melomys populations to fine-tune behavioral responses to be more predator specific through time. These behavioral shifts could reflect individual plasticity (phenotypic flexibility) in behavior or may be adaptive shifts from natural selection imposed by quoll predation. Our study provides a rare insight into the rapid ecological and behavioral shifts enacted by prey to mitigate the impacts of a novel predator and shows that trophic cascades can be strongly influenced by behavioral as well as numerical responses.

Key words: antipredator behavior; boldness; invasion; neophobia; predator–prey dynamics; prey naivety.

INTRODUCTION

Predation is one of the most pervasive and powerful forces acting on populations. Not only does predation directly impact a population's demography (Schoener and Spiller 1996), it also imposes natural selection (Abrams 2000). The pressure that predators impose on populations will vary through time and space for many reasons, including tightly coupled predator–prey dynamics, predator movement, prey switching, or stochastic processes (Lima and Dill 1990, Sih 1992). The fact that predation is not constant, and that antipredator defenses may be costly, suggests that flexible responses to predation pressure will often be evolutionarily favored (Sih

et al. 2000, Berger et al. 2001). There is, in fact, a great deal of empirical evidence that flexible responses to predation are common and vary with the perceived risk of predation (e.g., Relyea 2003, Brown et al. 2013, Cunningham et al. 2019).

Predators also play a powerful role in structuring communities (Estes et al. 2011). Some of our best evidence for this comes from the introduction of novel predators. Invasive predators can cause extinctions (Woinarski et al. 2015, Doherty et al. 2016), and alter trophic structures and ecosystem function within recipient communities (Courchamp et al. 2003, Simberloff et al. 2013). These cascading outcomes are often treated as purely numeric effects: predators depress the size of prey populations, and the altered numbers of prey can cause cascading numerical changes down trophic levels (Ripple et al. 2001). These numerical effects are undeniably important, but the fact that predators can also elicit phenotypic change in prey populations, through

Manuscript received 30 November 2020; revised 4 February 2021; accepted 22 February 2021. Corresponding Editor: Thomas J. Valone.

⁵E-mail: cjolly1@student.unimelb.edu.au

phenotypic plasticity and natural selection, means that subtler ecological effects may also manifest. Prey species living alongside predators may forage at different times, or in different places compared with the same species in a predator-free environment (Laundre et al. 2010). Such behavioral shifts can alter downstream species interactions in potentially complex ways (Fortin et al. 2005, Suraci et al. 2016, Atkins et al. 2019).

Because predator invasions are rarely intentional or anticipated, there is a paucity of controlled empirical work on the effects of novel predators on recipient communities and the mechanisms via which these effects play out (but see Lapedra et al. 2018, Pringle et al. 2019). Such tests are needed; however, if we are to predict invasive species impacts, and improve both conservation management (Sih et al. 2010a) and our understanding of how communities are structured (Sax et al. 2007).

Northern quolls (*Dasyurus hallucatus*) were, until recently, a common predator across northern Australia. They have declined over the last several decades, following the general decline in northern Australian mammals (Woinarski et al. 2015). More recently, the invasion of toxic invasive prey (cane toads, *Rhinella marina*) has resulted in dramatic, range-wide population declines in northern quolls (Moore et al. 2019). For their conservation, northern quolls have recently been introduced to a number of offshore islands where they have never previously existed.

In 2017, a population of 54 northern quolls were introduced to Indian Island (Kabarli), a 25-km² island off the coast of northwestern Northern Territory, Australia (Kelly et al. 2020). Prior to this introduction, Indian Island lacked mammalian predators, and large native reptilian predators had recently been reduced to near extinction by the invasion of cane toads. We take advantage of the introduction of northern quolls to a new island to directly test the effects of quolls as a novel predator on an island ecosystem and observe how native prey populations adjust to mitigate the impacts of their arrival. Quolls are an ecologically novel predator on this island but share an evolutionary history with its inhabitant prey species on the Australian mainland. Thus, we predict that this introduction may result in demographic effects (reduced survival and abundance) in invaded prey populations. If behavioral adjustments are able to reduce the demographic effects of a novel predator, we predict rapid behavioral changes in quoll-exposed melomys populations may manifest through time, such as changes in personality composition, foraging behavior, and responses to predator scent.

METHODS

Introduction of northern quolls

In May 2017, 54 adult northern quolls were introduced to the northeastern tip of Indian Island, Bynoe Harbor, Northern Territory, Australia (12°37′24.60″ S,

130°30′0.72″ E; see Appendix S1: Fig. S1). Quolls are a voracious, opportunistic, generalist predator (<1.5 kg; Oakwood 1997), and their introduction presented an opportunity to monitor the behavioral and demographic impacts on grassland melomys (*Melomys burtoni*), a native mammalian granivorous prey species (mean body mass 56 g, range 5.6–103.7 g). Logistical challenges prevented us from implementing a Before–After Control–Impact study design (see Appendix S1: Section S1). Here, we present data from before the introduction of quolls from one invaded site only. Most of our data compare quoll-invaded (impact) vs. quoll-free (control) sites over time, commencing within a few months of quoll arrival.

Melomys population monitoring

To determine whether the arrival of a novel predator resulted in demographic impacts (population size and survival) to a native prey species, we monitored four “impact,” quoll-invaded sites established in the north of Indian island in the vicinity of where quolls were released and three “control,” quoll-free sites established in the south of the island (Fig. 1). Populations of melomys on Indian Island were monitored during four trips occurring immediately prior to the introduction of quolls in May (site 1) 2017, and after the introduction of quolls August 2017 (sites 2–7), April 2018 (sites 1–7), and May 2019 (sites 1–7).

Melomys were monitored at seven independent 1-ha (100 × 100 m) plots (sites 1–7) spread out across Indian Island using a standard mark–recapture trapping regime designed for a monitoring project (Begg et al. 1983, Kemper et al. 1987). Sites in the north (quoll-invaded) and south (quoll-free) of the island were between 8.7 and 9.8 km apart (Fig. 1; Appendix S1: Table S1) and were composed of similar habitat types (see Appendix S1: Fig. S1) and exposed to near identical environmental conditions. The northern and southern sections of Indian Island are divided by mangrove habitat that is inundated at high tide. Cage and camera trapping as well as track surveys confirmed that quolls were present at the “impact” sites and absent from the “control” sites for the duration of the study (data not shown).

Each of the seven monitoring sites consisted of 100 Elliott traps (Elliott Scientific Equipment, Upwey, Victoria) spaced at 10-m intervals in a 10 × 10 grid. Most trapping grids were open for four nights; however, the first trapping grid (site 1, May 2017) was open for six nights (during pilot study). After four trap nights most captures were recaptures, therefore, the majority of the melomys population had been captured at least once and additional trap nights were not necessary (Jolly et al. 2019). Traps were baited with balls of peanut butter, rolled oats, and honey. These baits were replaced daily for the duration of each trapping session. Traps were checked for captures early each morning and all traps were cleared within 2 h of sunrise.

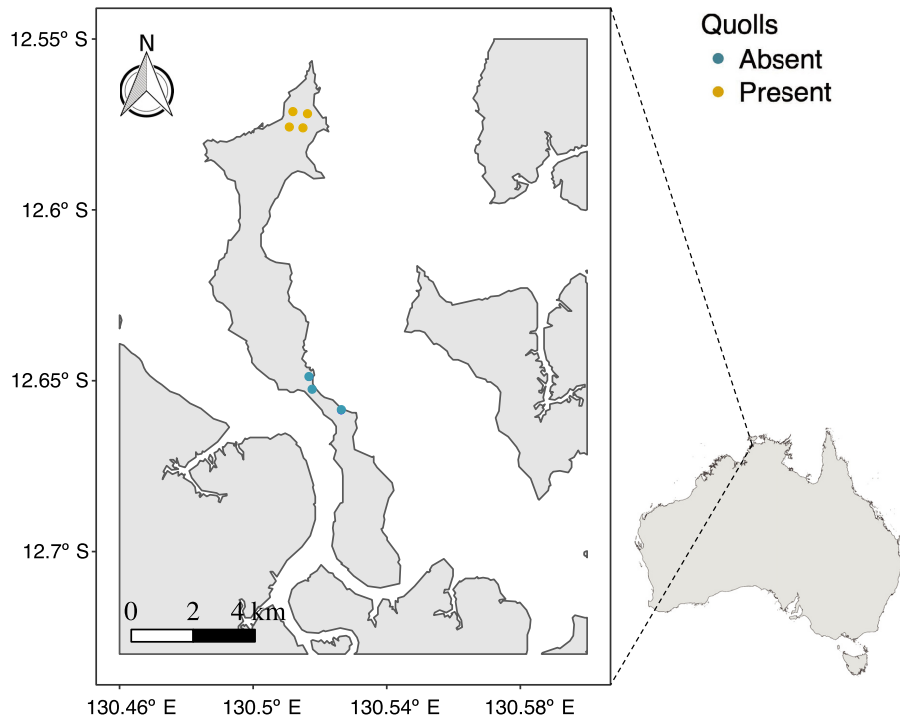


FIG. 1. Map showing the arrangement of grassland melomys (*Melomys burtoni*) monitoring sites on Indian Island, Northern Territory, Australia. Quolls were present at the four monitoring sites in the north of the island and quolls were absent from the three monitoring sites in the south of the island for the duration of the study.

Captured melomys were weighed (g) and sexed. Before release, each melomys was implanted with a microchip (Trovan Unique ID100, Trovan Ltd., Douglas, UK). On successive mornings, all melomys were scanned (Trovan LID575 Handheld Reader), and any new individuals were microchipped. On the last morning of each trapping session, all melomys caught were retained for behavioral assays. Throughout the study, 439 individual melomys were captured and given microchips (melomys caught per site: site 1, 83; site 2, 52; site 3, 63; site 4, 59; site 5, 69; site 6, 59; and site 7, 54). Of these, 191 (43%) were caught on the final night of trapping and were retained for behavioral trials. Only large, healthy juveniles ($n = 12$), adult males ($n = 83$), and adult non-visibly pregnant females ($n = 96$) were retained for behavioral experiments (see Appendix S1: Table S2). Melomys were retained in their respective Elliott traps and taken to the field station for diurnal husbandry. They were provided food and water ad libitum until 2 h prior to testing. At this point, in an attempt to standardize hunger levels, access to food and water was removed. Indian Island is remote and uninhabited by humans, so all behavioral experiments were conducted in the field under near natural conditions (see Jolly et al. [2019] for detailed experimental procedures).

Modified open field tests examining population behavior

We employed modified open field tests (also referred to as emergence tests; see López et al. 2005, Carter et al.

2013, Jolly et al. 2019) to assess boldness in grassland melomys and whether the arrival of a novel predator resulted in behavioral shifts in invaded populations (see Appendix S1: Fig. S2). All open field tests were conducted on the night after the last trap night (night 5) and in opaque-walled experimental arenas ($540 \times 340 \times 370$ mm). Experimental arenas were modified plastic boxes that had an inverted Elliott trap sized hole cut in one end and were illuminated by strings of red LED lights (Jolly et al. 2019). Each experimental arena had natural sand as substrate, and a rolled ball of universal bait (peanut butter, oats, and honey) located both in the center and along one wall of the arena (Jolly et al. 2019). After dark, Elliott traps containing a melomys were inserted into the hole in the side of each experimental arena and melomys were allowed to habituate for 10 minutes. At the start of each trial, Elliott trap doors were locked open; the inverted orientation of the trap prevented them from being triggered closed. Melomys were given 10 minutes to explore the open field arena. After 10 minutes, individuals were rounded back into their retreat (the Elliott trap) and a novel object (standard red, plastic, disposable bowl) was placed at the end of the arena opposite the Elliott trap (Jolly et al. 2019). Melomys were then given a further 10 minutes to explore the arena and interact with the novel object. Elliott traps remained open during the open field tests and melomys could shelter and emerge from them under their own volition. All trials were recorded using a

GoPro HERO 3 (GoPro Inc., San Mateo, CA, USA). A previous study in this system determined that individual melomys showed repeatable behavior between three repeat trials (interclass correlation coefficient (ICC) scores; boldness R [95% CI] = 0.67 [0.47, 0.80], $P < 0.001$; emergence time R [95% CI] = 0.73 [0.53, 0.83], $P < 0.001$; novel object R [95% CI] = 0.61 [0.209, 0.974], $P < 0.001$; Jolly et al. 2019). Therefore, the data presented in this study were from a single behavioral trial of each animal ($n = 146$). Once trials were complete, each melomys was released at its point of capture.

To measure the boldness of individual melomys, we scored three behaviors typically associated with boldness and neophobia in rodents (Dielenberg and McGregor 2001, McGregor et al. 2002, Réale et al. 2007, Cremona et al. 2015): whether melomys fully emerged from their Elliott trap hide and entered the open arena during the 0–10 min period (scored 0 or 1, respectively); whether they fully emerged and entered the trial arena during the 10–20 minute period (scored 0 or 1); and whether they interacted (touched) with the novel object that was placed in the arena during the 10–20 minute period (scored 0 or 1). Videos were scored by a single observer who was blind to each melomys' origin and identity. Because interacting with the novel object was predicated on a melomys' willingness to emerge from their hide during the 10–20 minute period, for analysis we combined their emergence during this period and interaction with the novel object into a single binary score: 0 (neophobic), did not emerge or emerged but did not interact with novel object; or 1 (not neophobic), emerged and interacted with novel object.

Seed-removal plots

To assess whether the arrival of a novel predator affected the seed harvesting behavior of granivorous melomys, we established seed removal plots at each site and sampled them after each trapping session (night 6). After trapping and open field tests were conducted and melomys had been returned to their capture location, we set up 81 seed plots at each site by scraping away leaf litter with a shovel to create bare earth plots ($\sim 30 \times 30$ cm). These bare earth plots were created so that they were located in the center between four Elliott traps within the 10×10 trapping grid. All seed plots were located randomly with respect to "distances to cover" but were all located on relatively open patches of ground. Sufficient within site replication ($n = 81$) significantly reduced the likelihood of distance to cover biasing population-level responses to seeds. Just before dark on the night of the seed removal experiment, we placed a single wheat seed in the center of each bare earth plot. These seeds were either unscented, control seeds ($n = 40$) or predator-scented seeds that had been maintained in a sealed clip-lock bag filled with freshly collected northern quoll fur ($n = 41$). The placement of predator-scented and unscented seeds was alternated so that there was a

checkered arrangement of scented and unscented seeds across the site. To ensure that the predator scent was strong enough to be detected by melomys, along with the predator-scented seeds, we also placed a few strands of quoll fur around the predator-scented seeds. Before light the next morning, we returned to each plot and counted the number of seeds of each scent type that were removed from the plot. Melomys are the only nocturnal granivorous animal that occurs on Indian Island; to avoid diurnal granivorous birds removing seeds, we conducted this experiment during the night only.

Wildfire on northern Indian Island

Immediately following our monitoring and experiments in August 2017, a wildfire broke out on northern Indian Island in the vicinity of the four quoll-invaded sites and burned through all of the sites. Because of this, our experimental design is confounded by the fact that all of our quoll-invaded sites were burned, and all of our quoll-free sites were unburned. Fire is a regular disturbance in this landscape (Andersen et al. 2005), and previous work has shown little effect of fire on abundance, survival, or recruitment of grassland melomys (Griffiths and Brook 2015, Liedloff et al. 2018). Nonetheless, this confound exists and we proceed with caution when interpreting the effects of quolls on population size and survival of melomys. This fire, however, is very unlikely to account for the differences we observe in melomys behavior between quoll-invaded and quoll-free sites, all of which were observed prior to and independently of the fire (see *Discussion*).

Statistical analysis

During trapping sessions, we identified individual melomys that were captured at each site by their unique microchips. Because melomys on Indian Island have very small home ranges (tending to be caught in the same or adjacent traps throughout the trapping period; data not shown) and since we never observed captures of melomys marked at other sites (data not shown), we treated each site as independent with regard to demographics and behavior (Fig. 1; Appendix S1: Table S1).

To estimate between-session survival, we analysed the mark–recapture data to estimate recapture and survival rates using Cormack–Jolly–Seber models in program MARK (see Appendix S1: Section S2).

To test whether the presence of quolls impacted melomys population size, we used a hierarchical model in which population size was made a function of quoll presence/absence, capture session, and the interaction between these factors. Population size at each site during each session is estimated in this process, and we fitted this model in a Bayesian framework (see Appendix S1: Section S2).

To assess whether the introduction of quolls affected the behavior of melomys populations, we divided the responses of melomys in open field tests into two

independent response variables: whether individuals emerged or not during the 0–10 minute period (binomial: 0 or 1); and whether individuals emerged and interacted with the novel object or not during the 10–20 minute period (binomial: 0 or 1). Because we only had comparable quoll present (impact) and quoll absent (control) behavioral data for sites 2–7, we excluded site 1 from this analysis (see Appendix S1; Fig. S3 for visual comparison of melomys behavior before and after the arrival of quolls). We used generalized linear mixed-effects models with binomial errors and a logit link to test the effect of quoll presence (two levels: quolls present and quolls absent) and trapping session (continuous), with site included as a random effect, on the behavioral response variables. Sex and mass were initially included as fixed effects with and without interaction terms but were removed from the model after they were found to have no effect. *P* values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect. This analysis was performed using R with the lme4 software package (Bates et al. 2015).

To assess whether the numerical impact of quolls on melomys affected the seed-harvesting rate of invaded melomys populations, we first examined the relationship between melomys population size (estimated above) and the total number of control (unscented) seeds harvested from each site. Here we used a simple linear model with number of seeds harvested as a linear function of population size, quoll presence/absence, and the interaction between these effects. To test whether there was an additional effect of quoll presence, beyond their effect on population size, we defined a new variable, Δ_{ks} , as the

difference in seed take between scented and unscented treatments within each site-session. Here any effect of melomys density is cancelled out (because density is common to both treatments within each site-session). Thus, we fitted a simple linear model in which Δ_{ks} is a function of quoll presence/absence, session and the interaction between these effects. All analyses were performed using R version 3.3.2 (R Core Team 2020).

RESULTS

Effect of novel predator on survival

The best supported model was one in which survival rates between sessions were lower at quoll-invaded sites than at quoll-free sites, and recapture rates were session dependent (see Appendix S1: Table S3). All other models were more than 4 AIC units from this best model, and so clearly inferior descriptions of the data. From the best-supported model, estimates of apparent survival (*S*) for the intervals between the capture sessions were substantially higher at quoll-free sites ($S_{2017-2018}$ [95% CI] = 0.368 [0.243, 0.515]; $S_{2018-2019}$ = 0.225 [0.138, 0.345]) than at quoll-invaded sites ($S_{2017-2018}$ = 0.207 [0.136, 0.303]; $S_{2018-2019}$ = 0.091 [0.041, 0.192]; Fig. 2). The differing survival probability between sessions is largely explained by the time difference between intervals (2017–2018 = 9 months vs. 2018–2019 = 13 months; Fig. 3).

Effect of novel predator on population size

Populations of melomys declined dramatically (by 45%) in quoll-invaded sites in the year following their

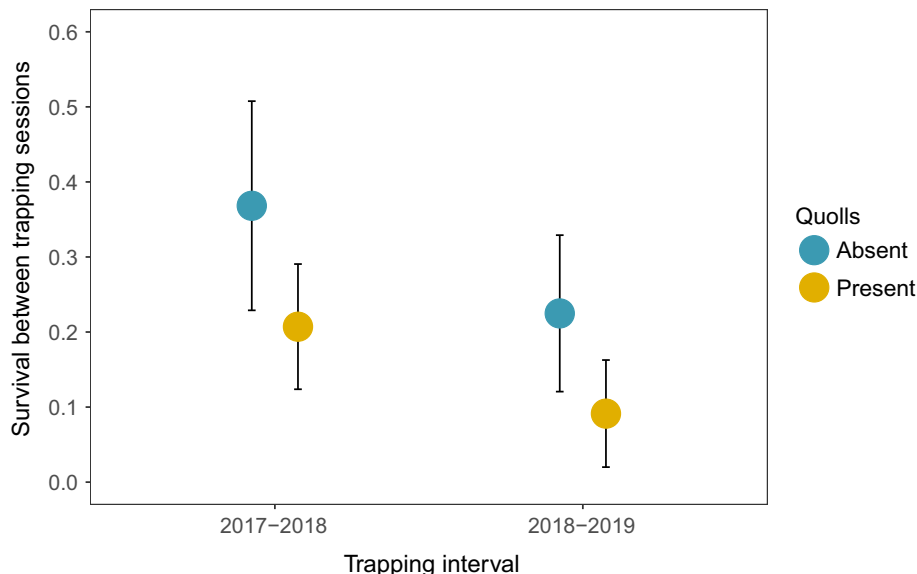


FIG. 2. Between trapping session survival (mean and 95% CI) of grassland melomys (*Melomys burtoni*) on Indian Island in quoll-invaded ($n = 4$) and quoll-free ($n = 3$) populations on Indian Island, Northern Territory, Australia.

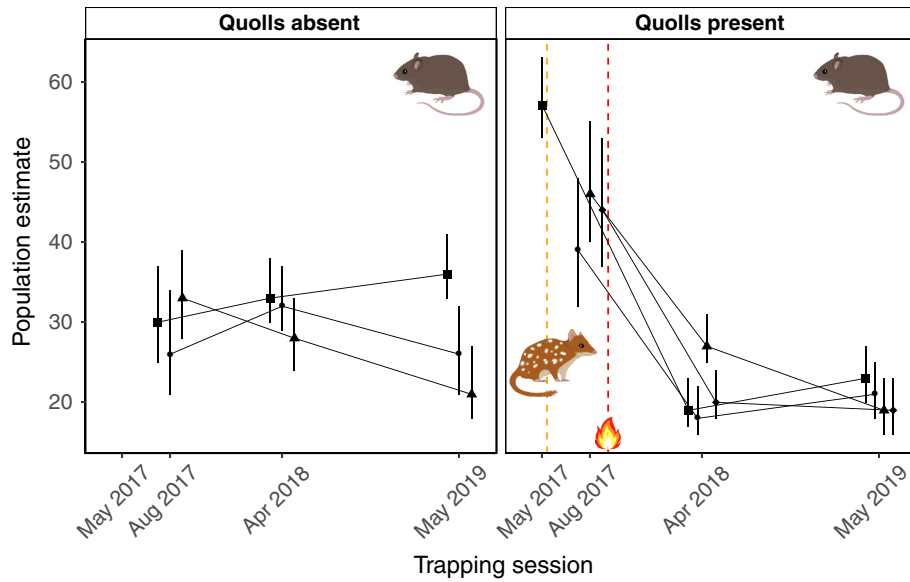


FIG. 3. Posterior mean population sizes (N_{ks} , and 95% CI) for quoll-invaded and quoll-free populations of grassland melomys (*Melomys burtoni*) on Indian Island, Northern Territory, Australia. The orange dotted vertical line denotes the timing of the introduction of quolls. The red-dotted vertical line denotes the timing of an unplanned fire that burned through the quoll-invaded sites. In each predator treatment, different sites are denoted by different-shaped points. Estimates assume closure of the population within each session and detection probability that varies across sessions.

introduction but not in quoll-free sites (Fig. 3). We observe a strong negative interaction between the presence of quolls and trapping session in 2018 (mean = -1.194 , 95% credible interval [-1.732 , -0.665]) and 2019 (mean = -1.097 , 95% confidence interval [-1.652 , -0.551]; Fig. 3; see Appendix S1: Table S4).

Effects of novel predator on prey behavior

For the proportion of melomys emerging in open field tests during the 0–10 minute period, there was a significant interaction between quoll presence and trapping session ($\chi^2(5) = 4.386$, $P = 0.04$; Fig. 4). There was no interaction between quoll presence and trapping session

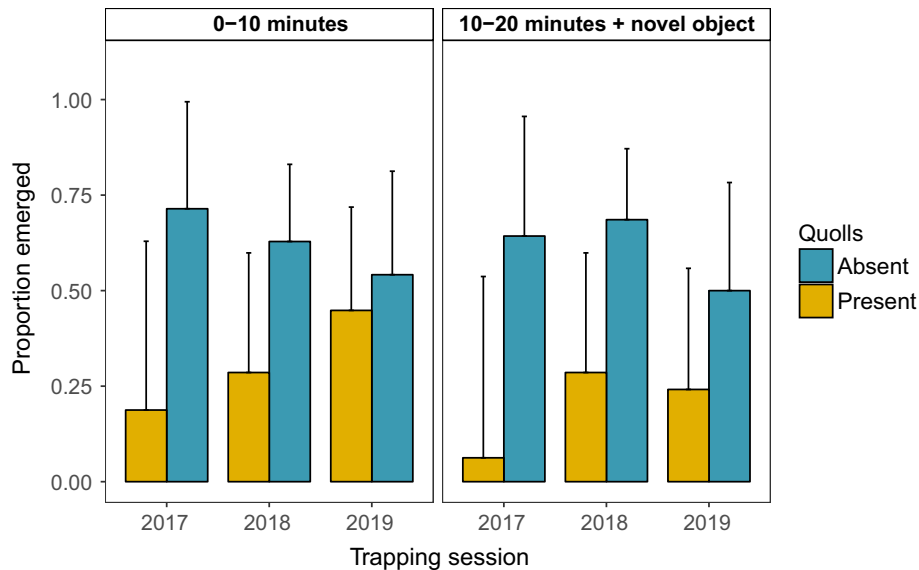


FIG. 4. Proportion (mean and 95% CI) of grassland melomys (*Melomys burtoni*) emerging from hiding during open field tests from quoll-invaded sites in 2017 ($n = 16$), 2018 ($n = 28$), and 2019 ($n = 29$) and quoll-free sites in 2017 ($n = 14$), 2018 ($n = 35$), and 2019 ($n = 24$) on Indian Island, Northern Territory, Australia.

for the proportion of melomys emerging and interacting with the novel object during a 10–20 minute period ($\chi^2(5) = 2.567$, $P = 0.109$; AIC = 181.98; Fig. 4). The model without this interaction, however, revealed a significant effect of quoll presence, with fewer melomys emerging from hiding and interacting with the novel object during the 10–20 minute period of open field tests from sites where quolls were present than from sites where quolls were absent ($\chi^2(5) = -4.696$, $P < 0.001$; AIC = 181.41; Fig. 4).

Effects of novel predator on seed harvesting and predator-scent aversion

Although there was no interaction between melomys density and quoll presence ($t_{18} = -0.251$, $P = 0.805$; Fig. 5A), there was a very clear positive relationship between melomys density and seed take ($t_{18} = 5.112$, $P < 0.001$; Fig. 5A) and a clear negative relationship between quoll presence and seed take ($t_{18} = -2.344$, $P = 0.031$; Fig. 5A). When we looked at the difference in seed take (Δ_{ks}) between scent treatments within a site-session, a striking pattern emerges, in which there is a clear interaction between the presence of quolls and session ($F_{3,17} = 18.61$, $P < 0.001$; Fig. 5B).

DISCUSSION

The introduction of northern quolls to Indian Island was associated with lowered survival and an apparent drop in population size in quoll-invaded melomys populations. This numerical effect on melomys density had an impact on seed predation rates, because seed take is strongly associated with the density of melomys in this system. This seems to be a classic trophic cascade: predation appears to suppress herbivore density, potentially reducing the pressure that herbivores place on primary producers. Our study, however, also reveals an

additional, subtler, cascade effect; driven by altered prey behavior rather than by altered prey density.

Within months of quolls appearing on the island, invaded populations of melomys were measurably shyer than nearby, predator-free populations of conspecifics. This rapid but generalized response to a novel threat appears to have had a subtle effect on seed predation rates: when we examine unscented seeds, per capita seed take is slightly lower in quoll-invaded populations. This generalized response appears to have been supplemented over time with more threat-specific antipredator behaviors. Although the boldness of predator-exposed melomys converged through time with that of predator-free melomys, predator-exposed melomys continued to be more neophobic than their predator-free conspecifics throughout the study. Meanwhile, predator-scent aversion, as evidenced by seed plots, steadily increased over time. Presumably the novel predation pressure imposed by quolls resulted in selection on behavior and/or learning in impacted rodent populations, allowing them to fine-tune their behavioral response (decrease general shyness, but maintain neophobia, and respond to specific cues) as the nature of the threat became clearer. These changing behavioral responses imply a generalized reduction in seed take that becomes fine-tuned over time, with high-risk sites (those that smell of predators) ultimately displaying substantially lower seed take than low risk sites. We see the emergence of a fine-scaled aversive response (varying on a spatial scale measured in the tens of meters) and affecting per capita rates of seed predation.

Although our study documented dramatic population declines in predator-invaded melomys populations, and we are assigning the primary cause of these declines to the introduction of quolls, we acknowledge there is potential for confounding factors to affect our results. We do not believe these confounds can explain our results, however. The primary confound is the

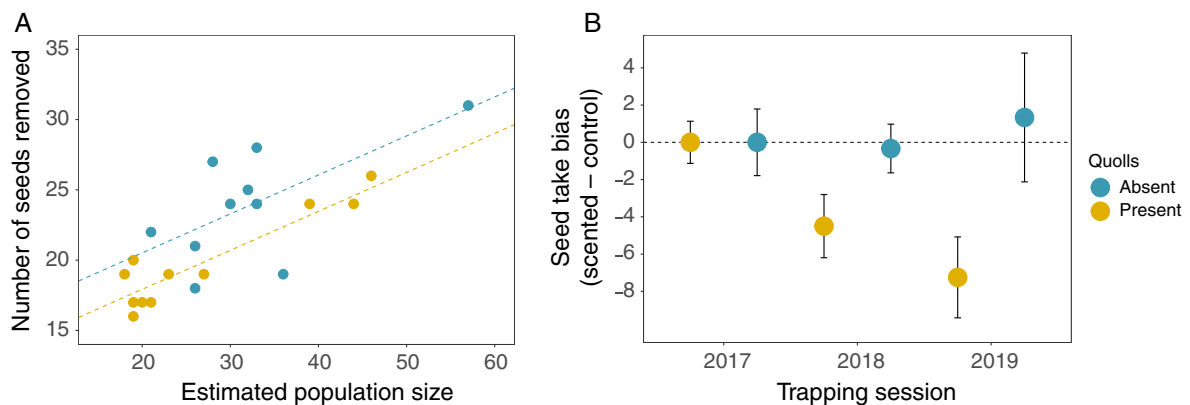


FIG. 5. (A) Effect of estimated population size on the number of control, unscented seeds removed from seed plots ($n = 21$) in quoll-invaded and quoll-free sites. Dotted lines denote the effect of quoll presence on seed removal rate. (B) Difference (Δ ; mean and 95% CI) between the number of predator-scented seeds and control, unscented seeds removed by melomys from quoll-invaded ($n = 3$, 2017 and $n = 4$, 2018–2019) and quoll-free ($n = 4$, 2017 and $n = 3$, 2018–2019) sites during each trapping session.

unplanned fire that burned through northern Indian Island after completion of our population monitoring in 2017 (also see Appendix S1: Section S3). Such fires are commonplace in the Australian wet-dry tropics (Russell-Smith and Yates 2007); a regular disturbance that is often rapidly offset by the annual monsoon driven wet season. Since our sites are composed of grass-free woodland (see Appendix S1: Fig. S1), the fire that burned through them mostly burned leaf litter (though it reached the mid-story in other parts of the island). While this likely reduced the short-term availability of food and cover for melomys, it is unlikely to directly explain the demographic effects we observed. A previous study investigating the effect of fire regimes on native mammals in savanna woodland in Kakadu National Park, Northern Territory was unable to detect an effect of fire frequency or intensity on the survival or recruitment of grassland melomys, despite finding fire impacts in all other co-occurring native mammals studied (Griffiths and Brook 2015). Interestingly, even in a system where fire is much more infrequent and significantly more intense (e.g., mesic habitats of eastern Australia), grassland melomys were found to be relatively unaffected by a wildfire that caused significant impacts to a co-occurring native rodent, and any demographic impacts felt by melomys were entirely absent within months of the fire (Liedloff et al. 2018). Additionally, the most dramatic behavioral difference (boldness and neophobia) between quoll-invaded and quoll-free sites was observed immediately prior to the occurrence of the fire (early August vs. mid-August 2017). For the behavioral changes we observed that were potentially confounded by fire, such as predator-scent aversion, we would expect to see these effects decreasing with time if fire was driving this response, instead we see the opposite trend. Finally, if food had become strongly limiting as a consequence of the fire, we would expect to have observed an increase in seed take in the burned (quoll-invaded) sites, instead we saw a decrease. For these reasons, we suspect the fire was unlikely to be directly responsible for the demographic effects to melomys we observed, and fire cannot in any way explain the response we observed to quoll-scented seeds. We, therefore, believe our interpretation of these changes, particularly the behavioral changes, as being driven mostly by the addition of a novel predator to the system is the most parsimonious and globally coherent interpretation of the data.

Predation is a pervasive selective force in most natural systems, driving evolutionary change in prey morphology, physiology, life history, and behavior. Unlike morphology and physiology, however, the labile nature of behavior makes it a particularly powerful trait for rapid response in a changing world (Réale et al. 2007, Sih et al. 2010b). Behavioral comparisons of wild populations exposed to differing predation regimes provides some support for the prediction that reduced boldness would be selected for under high predation scenarios (Åbjörnsson et al. 2004, Bell 2005, Brydges et al. 2008)

and that the appearance of novel predators can result in bold individuals becoming shyer (Niemelä et al. 2012). The opposite pattern (Brown et al. 2005, Urban 2007) or a non-response (Laurila 2000, Carlson and Langkilde 2014) can also occur, however. Interestingly, a number of studies have demonstrated that individuals from high-predation areas were quicker to emerge (Harris et al. 2010) and were bolder and more aggressive (Bell and Sih 2007, Dingemanse et al. 2007) than predator-naïve conspecifics. Although we found the opposite pattern to this immediately following the arrival of a novel predator, by the second year after predator introduction we found the boldness of melomys converging with that of predator-free populations. Thus, it is clear that the behavioral composition of these populations is dynamic, and it seems likely this dynamism (and perhaps the capacity of the prey species to identify specific threats) may explain some of the variation between earlier studies.

Although boldness may change over time, neophobia, as a generalized adaptive response to predation pressure, is now well supported across a number of studies (Crane et al. 2020). Individuals living under high predation risk scenarios have been shown to typically display generalized neophobia (Brown et al. 2015, Elvidge et al. 2016), and neophobia can increase the survival of predator-naïve individuals in initial encounters with predators (Ferrari et al. 2015, Crane et al. 2018). Certainly, in our study, predator-exposed melomys were significantly more neophobic than their predator-free conspecifics; an effect maintained throughout the study.

Despite reduced survival, significant population declines, and clear behavioral changes in invaded populations, it is impossible to determine from our data whether changes in the behavior of predator-invaded melomys populations are the result phenotypic plasticity (learning) or natural selection. The low between trapping session survival of melomys in quoll-invaded populations means few individuals survive between sessions, so natural selection is a possibility, and selection on these behavioral traits is potentially very strong. Although behavioral changes in predator-invaded populations have been documented in a few systems where predator introductions have been staged and experimentally controlled (Lapiedra et al. 2018, Blumstein et al. 2019, Cunningham et al. 2019, Pringle et al. 2019), elucidating whether these observed changes arise because of behavioral plasticity or natural selection can be exceptionally difficult. Rapid behavioral responses of vulnerable prey to recovered predators has been observed in a single prey generation, presumably due to behavioral plasticity (Berger et al. 2001, Cunningham et al. 2019). Similarly, behavioral adjustments to an introduced predator have been observed as a result of natural selection on advantageous behavioral traits (Lapiedra et al. 2018). In our study, we had measures of individual behavior, but our between session recapture rates of these individuals was too low to test whether individuals were altering their behavior or whether natural selection was resulting in population-

level change. It thus remains possible (and quite likely) that both mechanisms were in play.

Although northern quolls represent a novel predator to melomys on Indian Island, the two species' shared evolutionary history on the northern Australian mainland may provide some explanation as to why this staged introduction resulted in rapid, finely tuned, behavioral adjustment in melomys, rather than rapid local extinction (cf. Doody et al. 2017). Isolation from predators can result in rapid loss of antipredator behaviors from a prey species' behavioral repertoire (Blumstein and Daniel 2005, Jolly et al. 2018a, Jolly and Phillips 2021), dramatically increasing an individual's susceptibility to predation following the introduction of either predator or prey (Carthey and Banks 2014, Jolly et al. 2018b). But such outcomes are not inevitable: length of isolation, coevolutionary history, degree of predator novelty, density-dependent effects, population size, and pre-existing predator-prey associations (Berger et al. 2001, Blumstein 2006, Banks and Dickman 2007, Sih et al. 2010a, Carthey and Banks 2014) are all likely hugely influential in determining whether an invaded population adjusts to the invader or proceeds towards extinction. Recently, a conservation introduction of Tasmanian devils to an island previously lacking them found that their possum prey rapidly adjusted their foraging behavior to accommodate this newly arrived predator (Cunningham et al. 2019). Despite possums having lived on the island in isolation from devils since the 1950s, presumably, their long evolutionary history together on mainland Tasmania had them primed to respond to this predatory archetype (Sih et al. 2010a, Carthey and Banks 2014, Cunningham et al. 2019). This shared evolutionary history is likely responsible for both possums' and melomys' ability to rapidly mount appropriate antipredator responses. The predators are novel within an individual's lifetime, but the individual's ancestors have encountered them before.

Although our results suggest that invaded melomys populations are beginning to adjust to the presence of northern quolls, there has been no sign of demographic recovery on the island. Data from our seed removal experiment clearly demonstrated that the function of melomys as seed harvesters and dispersers scales with density. Trophic cascades resulting from the addition and loss of predators from ecosystems has been observed in a number of systems globally (Ripple et al. 2001, Terborgh et al. 2001, Estes et al. 2011), and the results can profoundly shape entire systems. As the only rodent and the dominant granivore in this system, while melomys populations may or may not go extinct as a result of quoll invasion, their reduced abundance and weakened ability to harvest and disperse seeds may have yet to be observed, longer-term consequences for the vegetation structure and ecosystem function of Indian Island (McConkey and O'Farrill 2016). Currently, grass is a rare vegetation feature on Indian island (though it is a dominant feature of nearby savanna woodlands on the

mainland), and this is quite possibly a result of the high density of melomys on this (previously) predator-free island. The presence of quolls may well change that, as both numerical and behavior responses of melomys cascade down to the grass community.

Empirical research on the effects of novel predators on recipient communities under controlled conditions on a landscape-scale is exceptionally difficult and remains relatively rare. The introduction of threatened predators to landscapes from which they have been lost (Cunningham et al. 2019) or where they are entirely novel (Lapiedra et al. 2018), however, provides a unique opportunity to observe how naïve prey can respond to novel predators, and the mechanisms by which predators can structure communities. Our study provides empirical support that some impacted prey populations can adjust rapidly to the arrival of a novel predator via a generalized behavioral response (decreased boldness) followed by development of a species-specific antipredator response (behavioral fine tuning). The arrival of the novel predator appears to have set off a trophic cascade that was driven, not only by changed prey density, but also by changed prey behavior. Thus, rapid adaptive shifts may allow prey populations to persist, but large-scale, system-wide changes may still follow.

ACKNOWLEDGMENTS

Thanks to Kenbi Traditional Owners (Raylene and Zoe Singh) for land access permission and Kenbi Rangers for assistance in the field. Special thanks to Kenbi Rangers (Brett Bigfoot, Rex Edmunds, Jack Gardner, Ian McFarlane, Dale Singh, and Rex Sing) for continued field assistance throughout this project. Thanks to Kenbi Ranger Coordinator Steven Brown for logistical support in the field. Thanks to Ella Kelly and Naomi Indigo for logistical and moral support on the island. Thanks to Alana de Laive for graphic design of figures. We thank two anonymous reviewers and D. Réale for their comments via Peer Community in Ecology, which greatly improved the manuscript. This research was funded by an Australian Research Council Linkage Grant (J. K. Webb and B. L. Phillips LP150100722). Animal ethics approval for this work was provided by the University of Melbourne (1814518) and Charles Darwin University (A13026) Animal Ethics Committees. In kind support was provided by Kenbi Rangers and the Northern Territory Government Department of Environment and Natural Resources, Flora and Fauna Division (via G. R. Gillespie). C. J. Jolly was supported by an Australian Postgraduate Award, the Holsworth Wildlife Research Endowment and David Hay Postgraduate Writing Up Award. Authorship statement: C. J. Jolly and B. L. Phillips designed the study; C. J. Jolly, A. S. Smart, J. Moreen, and B. L. Phillips collected data; C. J. Jolly and B. L. Phillips performed analyses and wrote the manuscript; all authors (except J. Moreen) contributed to revisions.

LITERATURE CITED

- Åbjörnsson, K., L.-A. Hansson, and C. Brönmark. 2004. Responses of prey from habitats with different predator regimes: local, adaptation and heritability. *Ecology* 85:1859–1866.
- Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.

- Andersen, A. N., G. D. Cook, L. K. Corbett, M. M. Douglas, R. W. Eager, J. Russell-Smith, S. A. Setterfield, R. J. Williams, and J. C. Z. Woinarski. 2005. Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* 30:155–167.
- Atkins, J. L., R. A. Long, J. Pansu, J. H. Daskin, A. B. Potter, M. E. Stalmans, C. E. Tarnita, and R. M. Pringle. 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* 364:173–177.
- Banks, P. B., and C. R. Dickman. 2007. Alien predation and the effects of multiple levels of prey naïveté. *Trends in Ecology & Evolution* 22:229–230.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Begg, R., B. Walsh, F. Woerle, and S. King. 1983. Ecology of *Melomys burtoni*, the grassland melomys (Rodentia: Muridae) at Cobourg Peninsula, N.T. *Wildlife Research* 10:259–267.
- Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*): behavioural syndromes. *Journal of Evolutionary Biology* 18:464–473.
- Bell, A. M., and A. Sih. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters* 10:828–834.
- Berger, J., J. E. Swenson, and I.-L. Persson. 2001. Recolonizing carnivores and naïve prey: conservation lessons from pleistocene extinctions. *Science* 291:1036–1039.
- Blumstein, D. T. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology* 112:209–217.
- Blumstein, D. T., and J. C. Daniel. 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B* 272:1663–1668.
- Blumstein, D. T., M. Letnic, and K. E. Moseby. 2019. *In situ* predator conditioning of naïve prey prior to reintroduction. *Philosophical Transactions of the Royal Society B* 374:20180058.
- Brown, C., F. Jones, and V. Braithwaite. 2005. *In situ* examination of boldness–shyness traits in the tropical poeciliid, *Brahyraphis episcope*. *Animal Behavior* 70:1003–1009.
- Brown, G. E., C. K. Elvidge, I. Ramnarine, M. C. O. Ferrari, and D. P. Chivers. 2015. Background risk and recent experience influences retention of neophobic responses to predators. *Behavioral Ecology and Sociobiology* 69:737–745.
- Brown, G. E., M. C. O. Ferrari, C. K. Elvidge, I. Ramnarine, and D. P. Chivers. 2013. Phenotypically plastic neophobia: a response to variable predation risk. *Proceedings of the Royal Society B* 280:20122712.
- Brydges, N. M., N. Colegrave, R. J. P. Heathcote, and V. A. Braithwaite. 2008. Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks. *Journal of Animal Ecology* 77:229–235.
- Carlson, B. E., and T. Langkilde. 2014. No evidence of selection by predators on tadpole boldness. *Behaviour* 151:23–45.
- Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlshaw, and R. Heinsohn. 2013. Animal personality: what are behavioural ecologists measuring? *Biological Reviews* 88:465–475.
- Carthey, A. J. R., and P. B. Banks. 2014. Naïveté in novel ecological interactions: lessons from theory and experimental evidence. *Biological Reviews* 89:932–949.
- Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78:347–383.
- Crane, A. L., G. E. Brown, D. P. Chivers, and M. C. O. Ferrari. 2020. An ecological framework of neophobia: from cells to organisms to populations. *Biological Reviews* 95:218–231.
- Crane, A. L., D. P. Chivers, and M. C. O. Ferrari. 2018. Embryonic background risk promotes the survival of tadpoles facing surface predators. *PLoS ONE* 13:e0193939.
- Cremona, T., V. S. A. Mella, J. K. Webb, and M. S. Crowther. 2015. Do individual differences in behavior influence wild rodents more than predation risk? *Journal of Mammalogy* 96:1337–1343.
- Cunningham, C. X., C. N. Johnson, T. Hollings, K. Kreger, and M. E. Jones. 2019. Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species. *Ecography* 42:2053–2059.
- Dielenberg, R. A., and I. S. McGregor. 2001. Defensive behavior in rats towards predatory odors: a review. *Neuroscience and Biobehavioral Reviews* 25:597–609.
- Dingemans, N. J., J. Wright, A. J. N. Kazem, D. K. Thomas, R. Hickling, and N. Dawnay. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology* 76:1128–1138.
- Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences USA* 113:11261–11265.
- Doody, J. S., D. Rhind, B. Green, C. Castellano, C. McHenry, and S. Clulow. 2017. Chronic effects of an invasive species on an animal community. *Ecology* 98:2093–2101.
- Elvidge, C. K., P. J. C. Chuard, and G. E. Brown. 2016. Local predation risk shapes spatial and foraging neophobia patterns in Trinidadian guppies. *Current Zoology* 62:457–462.
- Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Ferrari, M. C. O., M. I. McCormick, M. G. Meekan, and D. P. Chivers. 2015. Background level of risk and the survival of predator-naïve prey: can neophobia compensate for predator naïveté in juvenile coral reef fishes? *Proceedings of the Royal Society B* 282:20142197.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Griffiths, A. D., and B. W. Brook. 2015. Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere* 6:1–22.
- Harris, S., I. W. Ramnarine, H. G. Smith, and L. B. Pettersson. 2010. Picking personalities apart: estimating the influence of predation, sex and body size on boldness in the guppy *Poecilia reticulata*. *Oikos* 119:1711–1718.
- Jolly, C. J., J. K. Webb, and B. L. Phillips. 2018a. The perils of paradise: an endangered species conserved on an island loses antipredator behaviours within 13 generations. *Biology Letters* 14:20180222.c.
- Jolly, C. J., E. Kelly, G. R. Gillespie, B. Phillips, and J. K. Webb. 2018b. Out of the frying pan: Reintroduction of toad-smart northern quolls to southern Kakadu National Park. *Austral Ecology* 43:139–149.
- Jolly, C. J., and B. L. Phillips. 2021. Rapid evolution in predator-free conservation havens and its effects on endangered species recovery. *Conservation Biology* 35:383–385.
- Jolly, C. J., A. S. Smart, J. Moreen, J. K. Webb, G. R. Gillespie, and B. L. Phillips. 2020. Trophic cascade driven by behavioural fine-tuning as naïve prey rapidly adjust to a novel predator. *Zenodo*. <https://doi.org/10.5281/zenodo.3936466>.
- Jolly, C. J., J. K. Webb, G. R. Gillespie, N. K. Hughes, and B. L. Phillips. 2019. Bias averted: personality may not influence trappability. *Behavioral Ecology and Sociobiology* 73:129.

- Kelly, E., K. T. Owners, C. J. Rangers, N. Jolly, A. Indigo, J. W. Smart, and B. Phillips. 2020. No outbreeding depression in a trial of targeted gene flow in an endangered Australian marsupial. *Conservation Genetics* 22:23–33.
- Kemper, C. M., D. J. Kitchener, W. F. Humphreys, R. A. How, A. J. Bradley, and L. H. Schmitt. 1987. The demography and physiology of *Melomys* sp. (Rodentia: Muridae) in the Mitchell Plateau area, Kimberley, Western Australia. *Journal of Zoology* 212:533–562.
- Lapidra, O., T. W. Schoener, M. Leal, J. B. Losos, and J. J. Kolbe. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. *Science* 360:1017–1020.
- Laundre, J. W., L. Hernandez, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1–7.
- Laurila, A. 2000. Behavioural responses to predator chemical cues and local variation in antipredator performance in *Rana temporaria* tadpoles. *Oikos* 88:159–168.
- Liedloff, A. C., J. C. Wilson, and R. M. Engeman. 2018. The effect of wildfire on population dynamics for two native small mammal species in a coastal heathland in Queensland, Australia. *Acta Oecologica* 88:58–64.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- López, P., D. Hawlena, V. Polo, L. Amo, and J. Martín. 2005. Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. *Animal Behavior* 69:1–9.
- McConkey, K. R., and G. O’Farrill. 2016. Loss of seed dispersal before the loss of seed dispersers. *Biological Conservation* 201:38–49.
- McGregor, I. S., L. Schrama, P. Ambermoon, and R. A. Dielenberg. 2002. Not all ‘predator odours’ are equal: cat odour but not 2,4,5 trimethylthiazoline (TMT; fox odour) elicits specific defensive behaviours in rats. *Behavioral Brain Research* 129:1–16.
- Moore, H. A., J. A. Dunlop, L. E. Valentine, J. C. Z. Woinarski, E. G. Ritchie, D. M. Watson, and D. G. Nimmo. 2019. Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions* 25:1818–1831.
- Niemelä, P. T., N. DiRienzo, and A. V. Hedrick. 2012. Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. *Animal Behavior* 84:129–135.
- Oakwood, M. 1997. The ecology of the northern quoll, *Dasyurus hallucatus*. Thesis. Australian National University, Canberra, Australian Capital Territory Australia.
- Pringle, R. M., et al. 2019. Predator-induced collapse of niche structure and species coexistence. *Nature* 570:58–64.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemans. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- Relyea, R. A. 2003. Predators come and predators go: the reversibility of predator-induced traits. *Ecology* 84:1840–1848.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. *Biological Conservation* 102:227–234.
- Russell-Smith, J., and C. P. Yates. 2007. Australian savanna fire regimes: context, scales, patchiness. *Fire Ecology* 3:48–63.
- Sax, D., J. Stachowicz, J. Brown, J. Bruno, M. Dawson, S. Gaines, R. Grosberg, A. Hastings, R. Holt, and M. Mayfield. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* 22:465–471.
- Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381:691–694.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist* 139:1052–1069.
- Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010a. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119:610–621.
- Sih, A., J. Stamps, L. H. Yang, R. McElreath, and M. Ramenofsky. 2010b. Behavior as a key component of integrative biology in a human-altered world. *Integrative and Comparative Biology* 50:934–944.
- Sih, A., R. Ziemba, and K. C. Harding. 2000. New insights on how temporal variation in predation risk shapes prey behavior. *Trends in Ecology & Evolution* 15:3–4.
- Simberloff, D., et al. 2013. Impacts of biological invasions: what’s what and the way forward. *Trends in Ecology & Evolution* 28:58–66.
- Suraci, J. P., M. Clinchy, L. M. Dill, D. Roberts, and L. Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. *Nature Communications* 7:10698.
- Terborgh, J., et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.
- Urban, M. C. 2007. Risky prey behavior evolves in risky habitats. *Proceedings of the National Academy of Sciences USA* 104:14377–14382.
- Woinarski, J. C. Z., A. A. Burbidge, and P. L. Harrison. 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences USA* 112:4531–4540.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3363/supinfo>

OPEN RESEARCH

The data sets and code generated during this study (Jolly et al. 2020) are available on Zenodo: <http://doi.org/10.5281/zenodo.3936466>.