

1 **Trophic cascade driven by behavioural fine-tuning as naïve prey rapidly**
2 **adjust to a novel predator**

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23 **Keywords:** Antipredator behaviour, boldness, invasion, neophobia, novel predator,

24 predator-prey dynamics, prey naivety

25 **The arrival of novel predators can trigger trophic cascades driven by shifts in prey**
26 **numbers. Predators also elicit behavioural change in prey populations, via phenotypic**
27 **plasticity and/or rapid evolution, and such changes may also contribute to trophic**
28 **cascades. Here we document rapid demographic and behavioural changes in populations**
29 **of a prey species (grassland melomys *Melomys burtoni*, a granivorous rodent) following**
30 **the introduction of a novel marsupial predator (northern quoll *Dasyurus hallucatus*).**
31 **Within months of quolls appearing, populations of melomys exhibited reduced survival**
32 **and population declines relative to control populations. Quoll-invaded populations ($n = 4$)**
33 **were also significantly shyer than nearby, quoll-free populations ($n = 3$) of conspecifics.**
34 **This rapid but generalised response to a novel threat was replaced over the following two**
35 **years with more threat-specific antipredator behaviours (i.e. predator-scent aversion).**
36 **Predator-exposed populations, however, remained more neophobic than predator-free**
37 **populations throughout the study. These behavioural responses manifested rapidly in**
38 **changed rates of seed predation by melomys across treatments. Quoll-invaded melomys**
39 **populations exhibited lower per-capita seed take rates, and rapidly developed an**
40 **avoidance of seeds associated with quoll scent, with discrimination playing out over a**
41 **spatial scale of tens of metres. Presumably the significant and novel predation pressure**
42 **induced by quolls drove melomys populations to fine-tune behavioural responses to be**
43 **more predator-specific through time. These behavioural shifts could reflect individual**
44 **plasticity (phenotypic flexibility) in behaviour or may be adaptive shifts from natural**
45 **selection imposed by quoll predation. Our study provides a rare insight into the rapid**
46 **ecological and behavioural shifts enacted by prey to mitigate the impacts of a novel**
47 **predator and shows that trophic cascades can be strongly influenced by behavioural as**
48 **well as numerical responses.**

49 INTRODUCTION

50 Predation is one of the most pervasive and powerful forces acting on populations. Not only
51 does predation directly impact a population's demography (Schoener & Spiller 1996), it also
52 imposes natural selection (Abrams 2000). The pressure that predators impose on
53 populations will vary through time and space for many reasons, including tightly coupled
54 predator-prey dynamics, predator movement, prey switching, or stochastic processes (Lima
55 & Dill 1990; Sih 1992). The fact that predation is not constant, and that antipredator
56 defences may be costly, suggests that flexible responses to predation pressure will often be
57 favoured (Sih *et al.* 2000; Berger *et al.* 2001). There is, in fact, a great deal of empirical
58 evidence that flexible responses to predation are common (e.g. Relyea 2003; Brown *et al.*
59 2013; Cunningham *et al.* 2019). Investment in antipredator traits across morphology, life-
60 history, and behaviour often varies, and is dependent on the perceived risk of predation.

61 As well as impacting prey populations, it is increasingly apparent that predators play
62 a powerful role in structuring communities (Estes *et al.* 2011). Some of our best evidence for
63 this comes from the introduction of predators to naïve communities. Invasive predators can
64 cause extinctions (Medina *et al.* 2011; Woinarski *et al.* 2015; Doherty *et al.* 2016), and alter
65 trophic structures and ecosystem function within recipient communities (Courchamp *et al.*
66 2003; Simberloff *et al.* 2013). Cascading outcomes are often thought of as purely numeric
67 effects: predators depress the size of prey populations, and the altered numbers of prey can
68 cause cascading numerical changes down trophic levels (Ripple *et al.* 2001). These numerical
69 effects are undeniably important, but the fact that predators can also elicit phenotypic
70 change in prey populations—through phenotypic plasticity and natural selection—means
71 that subtler ecological effects may also manifest. Prey species living alongside predators
72 may forage at different times, or in different places compared with the same species in a

73 predator-free environment (Laundre *et al.* 2010). Such behavioural shifts can alter
74 downstream species interactions in potentially complex ways (Fortin *et al.* 2005; Suraci *et al.*
75 2016).

76 Because predator invasions are rarely intentional or anticipated, there is a scarcity of
77 controlled empirical work on the effects of novel predators on recipient communities and
78 the mechanisms via which these effects play out (but see Lapiedra *et al.* 2018; Pringle *et al.*
79 2019). Such tests are needed, however, if we are to predict invasive species impacts, and
80 improve conservation management (Sih *et al.* 2010a) and our understanding of how
81 communities are structured via predator invasion (Sax *et al.* 2007).

82 Northern quolls (*Dasyurus hallucatus*) were, until recently, a common predator
83 across northern Australia. They have declined over the last several decades, following the
84 general decline in northern Australian mammals (Woinarski *et al.* 2015), thought to be
85 driven by changes in grazing, fire, and predation regimes (Braithwaite & Griffiths 1994).
86 More recently, the invasion of toxic invasive prey (cane toads, *Rhinella marina*) has resulted
87 in dramatic, range-wide population declines in northern quolls (Shine 2010; Oakwood *et al.*
88 2016). Due to local extinction, northern quolls are now absent from large tracts of their
89 former range and their ecological function as a medium-sized mammalian predator has
90 been lost (Moore *et al.* 2019). For their conservation, northern quolls have recently been
91 introduced to a number of offshore islands where they have never previously existed.

92 In 2017, a population of 54 northern quolls were introduced to a 25km² island off the
93 coast of north-western Northern Territory, Australia (Kelly 2019). Prior to this introduction,
94 Indian Island (Kabarl) lacked mammalian predators, and large native reptilian predators had
95 recently been reduced to near extinction by the invasion of cane toads. We take advantage
96 of the introduction of northern quolls to a new island to directly test the effects of quolls as

97 a novel predator on an island ecosystem and observe how native prey populations adjust to
98 mitigate the impacts of their arrival. Since quolls are an ecologically novel predator on this
99 island, we predict that this introduction may result in demographic effects (reduced survival
100 and abundance) in invaded prey populations. If behavioural adjustments are able to reduce
101 the demographic effects of a novel predator, we predict rapid behavioural changes in quoll-
102 exposed melomys populations, such as changes in personality composition, foraging
103 behaviour and responses to predator-scent, may manifest through time.

104

105 **METHODS**

106 *Introduction of northern quolls*

107 In May 2017, 54 adult northern quolls were introduced to the north-eastern tip of Indian
108 Island, Bynoe Harbor, Northern Territory, Australia (12°37'24.60"S, 130°30'0.72"E) to field
109 test the conservation strategy of targeted gene flow (Kelly & Phillips 2016). Quolls are a
110 voracious, opportunistic generalist predator (< 1.5k g; Oakwood 1997), and their
111 introduction presented an opportunity to monitor the behavioural and demographic
112 impacts on grassland melomys (*Melomys burtoni*), a native mammalian granivorous prey
113 species (mean body mass 56 g, 5.6–103.7 g). Immediately prior to the introduction of quolls,
114 we started monitoring populations of melomys in one woodland and two monsoon vine
115 thicket plots in the vicinity of where quolls were to be released and radio tracked. After
116 quolls were introduced and tracked it became immediately apparent that quolls were
117 largely avoiding monsoon vine thicket sites and, since these sites would neither be effective
118 “impact” or “control” sites, these sites were dropped from the on-going monitoring.
119 Because these sites had to be dropped from our monitoring, we missed the opportunity to
120 implement a robust Before-After Impact-Control design. For this reason, we only present

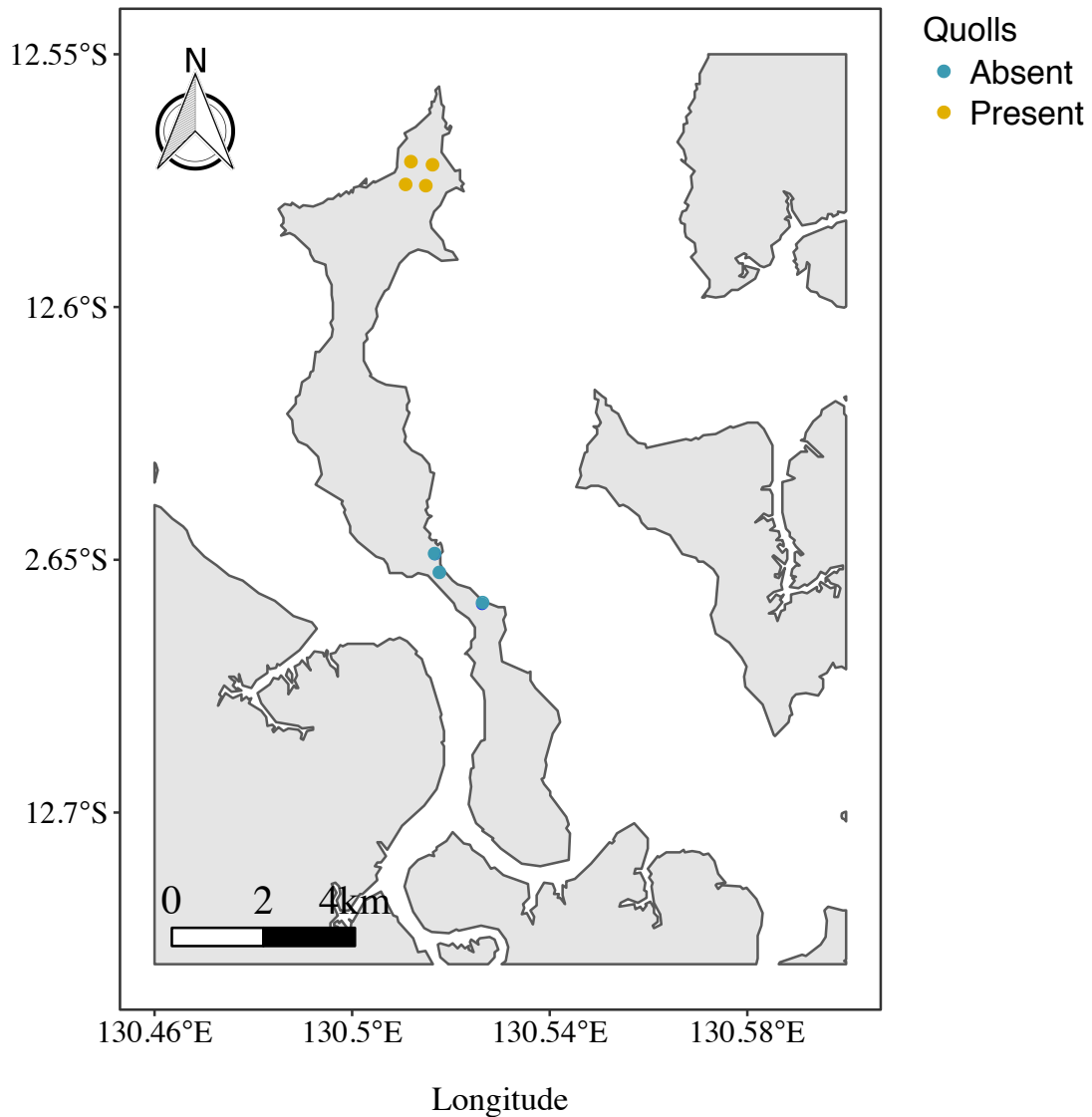
121 data from before the introduction of quolls from one invaded site. Most of our data
122 compare quoll-invaded (impact) versus quoll-free (control) sites over time, commencing
123 within a few months of quoll arrival.

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125 *Melomys population monitoring*

126 To determine whether the arrival of a novel predator resulted in demographic impacts
127 (population size and survival) to native prey species, we monitored four “impact”, quoll-
128 invaded sites established in the north of Indian island in the vicinity of where quolls were
129 released and three “control”, quoll-free sites established in the south of the island (Fig 1).
130 Populations of melomys on Indian Island were monitored during four trips occurring
131 immediately prior to the introduction of quolls in May (site 1) 2017, and after the
132 introduction of quolls August 2017 (sites 2–7), April 2018 (sites 1–7), and May 2019 (sites 1–
133 7).

134 Melomys were monitored at seven independent 1ha (100 m x 100 m) plots (sites 1–
135 7) spread out across Indian Island using a standard mark-recapture trapping regime
136 designed for a monitoring project (Begg *et al.* 1983; Kemper *et al.* 1987). Sites in the north
137 (quoll-invaded) and south (quoll-free) of the island were between 8.7 and 9.8km apart (Fig.
138 1; Table 1) and were composed of similar habitat types. The northern and southern sections
139 of Indian Island are divided by mangrove habitat which is inundated at high tide. Cage and
140 camera trapping as well as track surveys confirmed that quolls were present at the “impact”
141 sites and absent from the “control” sites for the duration of the study (Jolly *et al.* unpub.
142 data).



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144 **Figure 1.** Map showing the arrangement of grassland melomys (*Melomys burtoni*) monitoring sites on Indian

145 Island, Northern Territory, Australia. Quolls were present at the four monitoring sites in the north of the island

146 and quolls were absent from the three monitoring sites in the south of the island for the duration of the study.

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154 **Table 1.** Pairwise distance matrix between sites on Indian Island, Northern Territory, Australia. Quolls were
155 present at sites 1–4 and quolls were absent at sites 5–7 for the duration of the study.

Distance (m)	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Site 1							
Site 2	270						
Site 3	260	350					
Site 4	400	300	250				
Site 5	8760	9030	8710	9000			
Site 6	8470	8730	8450	8070	300		
Site 7	9670	9920	9590	9820	1260	1500	

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157 Each of the seven monitoring sites consisted of 100 Elliott traps (Elliott Scientific
158 Equipment, Upwey, Victoria) spaced at 10 m intervals in a 10 x 10 grid. Most trapping grids
159 were open for four nights, however, the first trapping grid (site 1, May 2017) was open for
160 six nights. After four trap nights, the majority of the melomys population had been captured
161 at least once (Jolly *et al.* 2019). Traps were baited with balls of peanut butter, rolled oats
162 and honey. These baits were replaced daily for the duration of each trapping session. Traps
163 were checked for captures early each morning and all traps were cleared within two hours
164 of sunrise.

165 Captured melomys were weighed (g) and sexed. Before release, each melomys was
166 implanted with a microchip (Trovan Unique ID100). On successive mornings, all melomys
167 were scanned (Trovan LID575 Handheld Reader), and any new individuals were
168 microchipped. On the last morning of each trapping session, all melomys caught were
169 retained for behavioural assays. Throughout the study 439 individual melomys were
170 captured and given microchips (melomys caught per site: site 1 = 83; site 2 = 52; site 3 = 63;
171 site 4 = 59; site 5 = 69; site 6 = 59; and site 7 = 54). Of these, 146 (33%) were caught on the
172 final night of trapping and were retained for behavioural trials. Only large, healthy juveniles
173 ($n = 11$), adult males ($n = 58$), and adult non-visibly pregnant females ($n = 77$) were retained

174 for behavioural experiments. Melomys were retained in their respective Elliott traps and
175 taken to the field station for diurnal husbandry. They were provided food and water *ad*
176 *libitum* until 2 hours prior to testing. At this point, in an attempt to standardise hunger
177 levels, access to food and water was removed. Indian Island is remote and uninhabited by
178 humans, so all behavioural experiments were conducted in the field under near natural
179 conditions (see Jolly *et al.* 2019 for detailed experimental procedures).

180

181 *Modified open field tests*

182 We employed modified open field tests (also referred to as emergence tests: see Brown &
183 Braithwaite 2004; López *et al.* 2005; Carter *et al.* 2013; Jolly *et al.* 2019) to assess boldness
184 in grassland melomys and whether the arrival of a novel predator resulted in behavioural
185 shifts in invaded populations. All open field tests were conducted on the night after the last
186 trap night (night 5) and in opaque-walled experimental arenas (540mm x 340mm x 370mm).
187 Experimental arenas were modified plastic boxes that had an inverted Elliott trap sized hole
188 cut in one end and were illuminated by strings of red LED lights (Jolly *et al.* 2019). Each
189 experimental arena had natural sand as substrate, and a rolled ball of universal bait (peanut
190 butter, oats and honey) located both in the centre and along one wall of the arena (Jolly *et*
191 *al.* 2019). After dark, Elliott traps containing a melomys were inserted into the hole in the
192 side of each experimental arena and melomys were allowed to habituate for 10 min. At the
193 start of each trial, Elliott trap doors were locked open—the inverted orientation of the trap
194 prevented them from being triggered closed. Melomys were given 10 min to explore the
195 open field arena. After 10 min, individuals were rounded back into their retreat (the Elliott
196 trap) and a novel object (standard red, plastic disposable bowl) was placed at the end of the
197 arena opposite the Elliott trap (Jolly *et al.* 2019). Melomys were then given a further 10 min

198 to explore the arena and interact with the novel object. Elliott traps remained open during
199 the open field tests and melomys could shelter and emerge from them under their own
200 volition. All trials were recorded using a GoPro HERO 3. A previous study in this system
201 determined that melomys showed repeatable behaviour between trials (boldness: R [\pm
202 95%CI] = 0.67 [0.47, 0.80], $P < 0.001$; emergence time: R [\pm 95%CI] = 0.73 [0.53, 0.83], $P <$
203 0.001; novel object: R [\pm 95%CI] = 0.61 [0.209, 0.974], $P < 0.001$; Jolly *et al.* 2019), therefore
204 the data presented in this study were from a single behavioural trial of each animal ($n =$
205 146). Once trials were complete, each melomys was released at its point of capture.

206 To measure the boldness of individual melomys, we scored three behaviours
207 typically associated with boldness and neophobia in rodents (Dielenberg & McGregor 2001;
208 McGregor *et al.* 2002; Réale *et al.* 2007; Cremona *et al.* 2015): whether melomys fully
209 emerged from their Elliott trap hide and entered the open arena during the 0–10 min period
210 (scored 0 or 1, respectively); whether they fully emerged and entered the trial arena during
211 the 10–20 min period (scored 0 or 1); and whether they interacted (touched) with the novel
212 object that was placed in the arena during the 10–20 min period (scored 0 or 1). Videos
213 were scored by a single observer who was blind to each melomys' origin and identity.
214 Because interacting with the novel object was predicated on a melomys' willingness to
215 emerge from their hide during the 10–20 min period, for analysis we combined their
216 emergence during this period and interaction with the novel object into a single binary
217 score: 0 (neophobic) = did not emerge or emerged but did not interact with novel object; or
218 1 (not neophobic): emerged and interacted with novel object.

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222 *Seed removal plots*

223 To assess whether the arrival of a novel predator affected the seed harvesting behaviour of
224 granivorous melomys, we established seed removal plots at each site and sampled them
225 each trapping session (night 6). After trapping and open field tests were conducted and
226 melomys had been returned to their capture location, we set up 81 seed plots at each site
227 by scraping away leaf litter with a shovel to create bare earth plots. These bare earth plots
228 were created so that they were located in the centre between four Elliott traps within the
229 10x10 trapping grid. All seed plots were located randomly with respect to “distances to
230 cover” but were all located on relatively open patches of ground. Sufficient within site
231 replication ($n = 81$) significantly reduces the likelihood of distance to cover biasing
232 population-level responses to seeds. Just before dark on the night of the seed removal
233 experiment, we placed a single wheat seed in the centre of each bare earth plot. These
234 seeds were either unscented, control seeds ($n = 40$) or predator-scented seeds that had
235 been maintained in a sealed clip-lock bag filled with freshly collected northern quoll fur ($n =$
236 41). The placement of predator-scented and unscented seeds was alternated so that there
237 was a chequered arrangement of scented and unscented seeds across the site. To ensure
238 that the predator-scent was strong enough to be detected by melomys, along with the
239 predator-scented seeds, we also placed a few strands of quoll fur around the predator-
240 scented seeds. Before light the next morning, we returned back to each plot and counted
241 the number of seeds of each scent-type that were removed from the plot. Melomys are the
242 only nocturnal granivorous animal that occurs on Indian Island, and to avoid diurnal
243 granivorous birds from removing seeds we conducted this experiment during the night only.

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246 *Wildfire on northern Indian Island*

247 Immediately following our monitoring and experiments in August 2017, a wildfire broke out
248 on northern Indian Island in the vicinity of the four quoll-invaded sites and burnt through all
249 of the sites. Because of this, our experimental design is confounded by the fact that all of
250 our quoll-invaded sites were burnt, and all of our quoll-free sites were unburnt. Fire is a
251 regular disturbance in this landscape (Andersen *et al.* 2005), and previous work has shown
252 little effect of fire on abundance, survival or recruitment of grassland melomys (Griffiths &
253 Brook 2015; Liedloff *et al.* 2018). Nonetheless, this confound exists and we proceed with
254 caution when interpreting the effects of quolls on population size and survival of melomys.

255

256 *Statistical analysis*

257 During trapping sessions we identified individual melomys that were captured at each site
258 by their unique microchips. Because melomys on Indian Island have very small home ranges
259 (tending to be caught in the same or adjacent traps throughout the trapping period: Jolly *et al.*
260 *al.* unpub. data) and since we never observed captures of melomys marked at other sites
261 (Jolly *et al.* unpub. data), we treated each site as independent with regard to demographics
262 and behaviour (Table 1).

263 To estimate between-session survival, we analysed the mark-recapture data to
264 estimate recapture and survival rates using Cormack-Jolly-Seber models in program MARK.
265 At each site, there were three primary trapping sessions of four nights, for a total of 12 time
266 intervals in the input file. Because quolls prey on melomys, we hypothesised that survival
267 rates of melomys would be lower between trapping sessions at sites with quolls than at
268 sites without quolls. We included two groups, quoll-free (control) and quoll-invaded
269 (impact), in the input file. We ran a series of models in MARK to test the following *a priori*

270 hypotheses: (1) survival rates between sessions are lower at quoll-free sites than at quoll-
271 invaded sites; (2) survival rates are lower between sessions than within sessions, but are
272 unaffected by quolls; (3) survival is constant through time; and (4) survival varies through
273 time. All candidate models were ranked according to their AICc values and associated AIC
274 weights (Burnham & Anderson 1998). Models with AICc values < 2 were considered to be
275 well supported by the data (Burnham & Anderson 1998). We used Akaike's Weights, which
276 are proportional to the normalized, relative likelihood of each model, and to determine
277 which of these models was most plausible (Buckland *et al.* 1997).

278 To test whether the presence of quolls impacted melomys population size, we used
279 a hierarchical model in which population size was made a function of quoll
280 presence/absence, capture session, and the interaction between these factors. Population
281 size at each site during each session is estimated in this process, and we fitted this model in
282 a Bayesian framework. Our observations consisted of a capture history for each observed
283 individual over the number of nights at each site for each trapping session. We denoted the
284 number of individuals at site s during session k as N_{ks} . To estimate N_{ks} we used a closed
285 population mark-recapture analysis in which each individual, i , was either observed, or not
286 (O_{iks}), according to a Bernoulli distribution:

$$287 \quad O_{iks} \sim \text{Bernoulli}(d_s)$$

288 Where d_s denotes the expected detection probability within session s . Our previous MARK
289 analysis found clear evidence for variation in detection probability across sessions, but
290 detection probabilities of melomys on Indian Island had previously been found not to vary
291 measurably between individuals nor to change over time within a trapping session (Jolly *et*
292 *al.* 2019). Thus, we made detection probability a function of session according to:

$$293 \quad \text{logit}(d_s) = \mu_d + t_s$$

294 Where μ_d is the expected detection probability in the first session, and t_s denotes the
295 (categorical) effect of session on detection.

296 We used the “data augmentation” method (Tanner & Wong 1987; Royle *et al.* 2007;
297 Kery & Schaub 2011) in combination with this detection probability to estimate N_{ks} for each
298 site per session (site.session). Using this approach, the data were ‘padded’ to a given size by
299 adding an arbitrary number of zero-only encounter histories of ‘potential’ unobserved
300 individuals. The augmented dataset was then modelled as a zero-inflated model (Royle *et al.*
301 2007) which changes the problem from estimating a count, to estimating a proportion. This
302 was executed by adding a latent binary indicator variable, R_{iks} , (taking values of either 0 or 1)
303 to classify each row in the augmented data matrix as a ‘real’ individual or not, where $R_{iks} \sim$
304 Bernoulli(Ω_{ks}). The parameter Ω_{ks} is the proportion of the padded population that is real,
305 and $N_{ks} = \sum_i R_{iks}$.

306 We then made Ω_{ks} (which scales with population size) a function of quoll
307 presence/absence, q_c ; session, b_k ; and the interaction between the two:

$$308 \quad \text{logit}(\Omega_{ks}) = \mu_p + q_c + b_k + \gamma_{ck}$$

309 The model was fitted using Bayesian Markov Chain Monte Carlo (MCMC) methods
310 and minimally informative priors (Table 2) within the package JAGS (Plummer *et al.* 2017)
311 using R (R Core Team 2019). Parameter estimates were based on 30,000 iterations with a
312 thinning interval of 5 following a 10,000 sample burn-in. Three MCMC chains were run, and
313 model convergence assessed by eye, and using the Gelman-Rubin diagnostic (Gelman &
314 Rubin 1992a, 1992b).

315 To assess whether the introduction of quolls affected the behaviour of melomys
316 populations, we divided the responses of melomys in open field tests into two independent
317 response variables: whether individuals emerged or not during the 0-10 min period

318 (binomial: 0 or 1); and whether individuals emerged and interacted with the novel object or
319 not during the 10-20 min period (binomial: 0 or 1). We used generalised linear mixed-effects
320 models with binomial errors and a logit link to test the effect of quoll presence (two levels:
321 quolls present and quolls absent) and trapping session (continuous), with site included as a
322 random effect, on the behavioural response variables. *P*-values were obtained by likelihood
323 ratio tests of the full model with the effect in question against the model without the effect.
324 This analysis was performed using R with the *lme4* software package (R Core Team 2019).

325 To assess whether the numerical impact of quolls on melomys affected the seed
326 harvesting rate of invaded melomys populations, we first examined the relationship
327 between melomys population size (estimated above) and the total number of control
328 (unscented) seeds harvested from each site. Here we used a simple linear model with
329 number of seeds harvested as a linear function of population size, quoll presence/absence
330 and the interaction between these effects. To test whether there was an additional effect of
331 quoll presence, beyond their effect on population size, we defined a new variable, Δ_{ks} , as
332 the difference in seed take between scented and unscented treatments within each
333 site.session. Here any effect of melomys density is cancelled out (because density is
334 common to both treatments within each site.session). Thus, we fitted a model in which Δ_{ks}
335 is a function of quoll presence/absence, session and the interaction between these effects.
336 These analyses were performed using R version 3.3.2 (R Core Team 2019).

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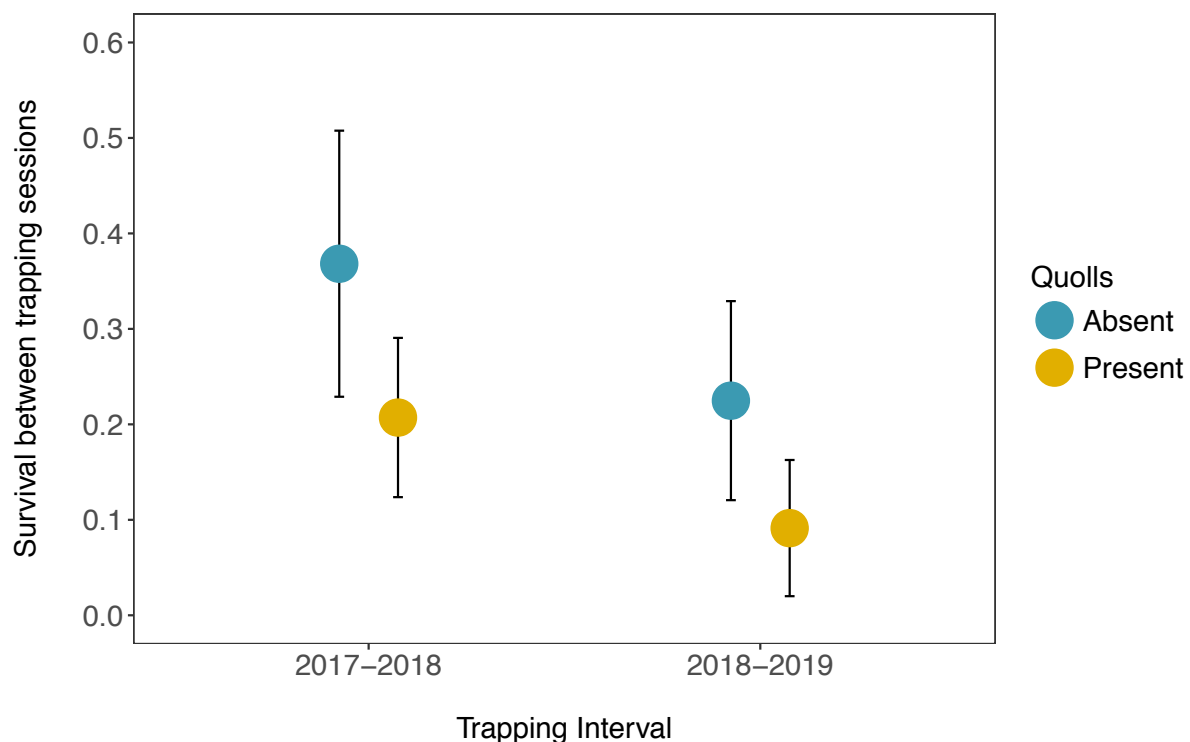
338 **RESULTS**

339 *Effect of novel predator on survival*

340 When we assessed the impact of quolls on melomys survival between trapping sessions the
341 best supported model was one in which survival rates between sessions were lower at

342 quoll-invaded sites than at quoll-free sites, and recapture rates were session-dependent
343 (Table 2). All other models were more than 4 AIC units from this best model, and so clearly
344 inferior descriptions of the data. From the best-supported model, estimates of apparent
345 survival (S) for the intervals between the capture sessions were substantially higher at
346 quoll-free sites ($S_{2017-2018} = 0.368$; $S_{2018-2019} = 0.225$) than at quoll-invaded sites ($S_{2017-2018} =$
347 0.207 ; $S_{2018-2019} = 0.091$; Fig. 2). The differing survival probability between sessions is
348 largely explained by the time difference between intervals (2017–2018 = 9 months vs.
349 2018–2019 = 13 months; Fig. 3).

350



351

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

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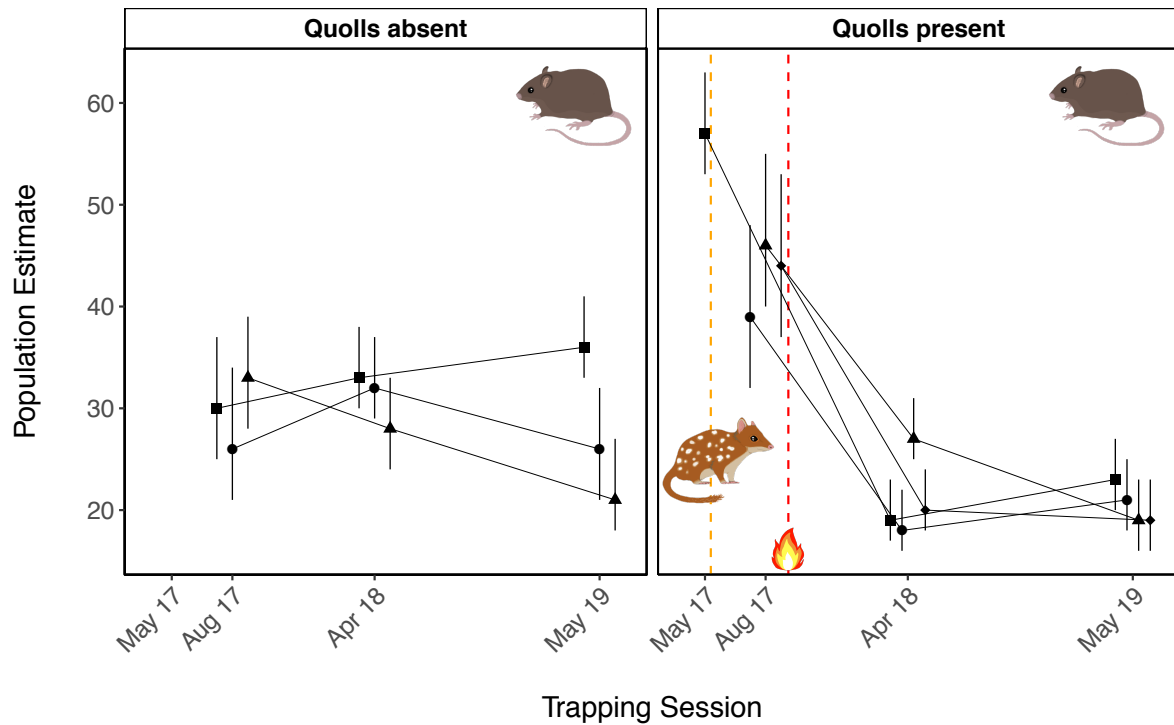
357 **Table 2.** Results of Cormack-Jolly-Seber analyses used to compare survival (Φ) and recapture (p) probabilities
 358 of grassland melomys (*Melomys burtoni*) on Indian Island, Northern Territory, Australia. The symbols ‘.’ and ‘t’
 359 refer to constant and time, respectively, while ‘g’ denotes the two groups (quoll free versus quolls present).
 360 Table shows AIC values and associated AIC weights, model likelihood, number of parameters (N), and model
 361 deviance. The term ‘w/b’ indicates that within trapping session survival rates (s_1 - s_3 , s_5 - s_7 , s_9 - s_{11}) were constant
 362 and equivalent, and different to the between trapping session survival rates (s_4 , s_8). The term ‘group w/b’ is as
 363 above, except that between trapping session survival rates differed between the two groups.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	N	Deviance
Phi (group w/b) p(t)	1688.629	0	0.92162	1	16	477.5224
Phi (w/b) p(t)	1693.562	4.933	0.07823	0.0849	14	486.6202
Phi (group w/b) p(g x t)	1701.116	12.4873	0.00179	0.0019	27	466.705
Phi (group w/b) p(g x t)	1703.132	14.503	0.00065	0.0007	7	510.5963
Phi (t) p (g*t)	1718.863	30.2344	0	0	32	473.631
Phi (t) p (.)	1719.862	31.2339	0	0	12	517.0641
Phi (t) p (g)	1720.751	32.1229	0	0	13	515.8843

364

365 *Effect of novel predator on population size*

366 Populations of melomys declined dramatically in quoll-invaded sites in the year following
 367 their introduction but not in quoll-free sites (Fig. 3). We observe a strong negative
 368 interaction between the presence of quolls and trapping session in 2018 (mean = -1.194,
 369 95% credible interval [-1.732, -0.665]) and 2019 (mean = -1.097, 95% confidence interval [-
 370 1.652, -0.551]; Fig. 3; Table 3).



371

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

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386 **Table 3.** Model parameters and their priors including prior distributions, standard deviation, estimated
 387 posterior means and their 95% credible intervals. N denotes normal probability distribution with mean and
 388 standard deviation.

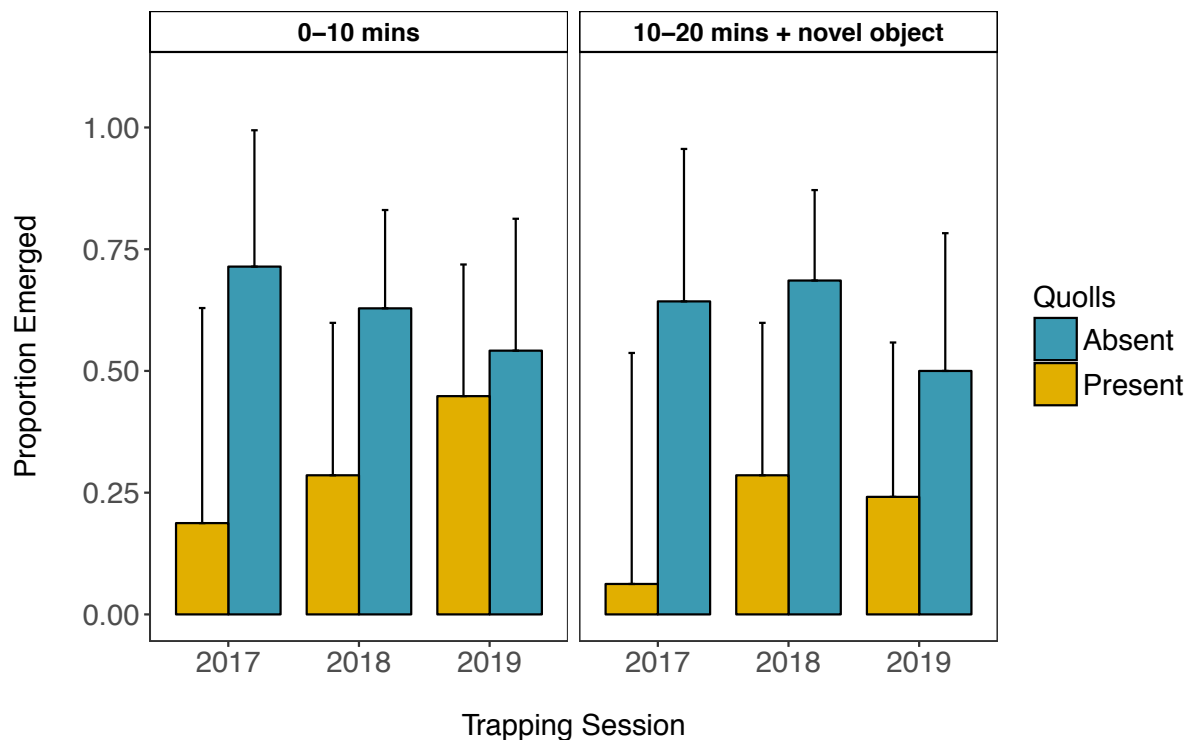
Model Parameters				
Name for parameter	Parameter	Prior (mean, SD)	Posterior mean	95% credible intervals
Detection:				
Intercept for detection	μ_d	N (0, 2.71)	-0.94	-1.12, -0.76
Effect of session 2 on detection	t_2	N (0, 2.71)	0.59	0.33, 0.85
Effect of session 3 on detection	t_3	N (0, 2.71)	0.46	0.18, 0.73
Population size:				
Intercept for Omega	μ_p	N (0, 2.71)	-0.91	-1.22, -0.58
Quoll Presence	r_2	N (0, 2.71)	0.70	0.31, 1.09
Trapping Session 2	b_2	N (0, 2.71)	0.06	-0.36, 0.48
Trapping Session 3	b_3	N (0, 2.71)	-0.10	-0.53, 0.34
Interaction 1 [Quoll Presence * Trapping Session 2]	$\gamma_{2,2}$	N (0, 2.71)	-1.19	-1.73, -0.67
Interaction 2 [Quoll Presence * Trapping Session 3]	$\gamma_{2,3}$	N (0, 2.71)	-1.10	-1.65, -0.55

389

390 *Effects of novel predator on prey behaviour*

391 For the proportion of melomys emerging in open field tests during the 0–10 min period,
 392 there was a significant interaction between quoll presence and trapping session (χ^2 (5) =
 393 4.386, P = 0.04; Fig. 4). There was no interaction between quoll presence and trapping
 394 session for the proportion of melomys emerging and interacting with the novel object
 395 during 10–20 min period (χ^2 (5) = 2.567, P = 0.109; Fig. 4). The model without this

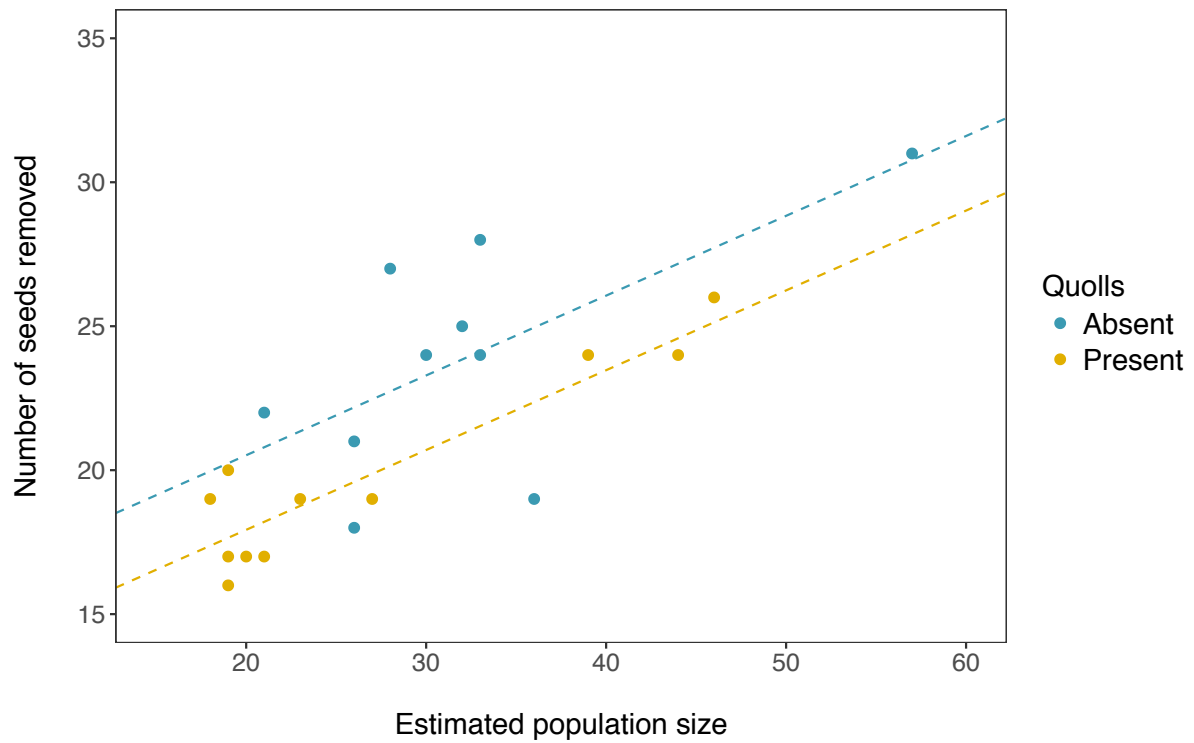
396 interaction, however, revealed a significant effect of quoll presence, with fewer melomys
397 emerging from hiding and interacting with the novel object during the 10–20 min period of
398 open field tests from sites where quolls were present than from sites where quolls were
399 absent ($\chi^2(5) = -4.696, P < 0.001$; Fig. 4).
400



401
402 **Figure 4.** Mean proportion (\pm 95% CI) of grassland melomys (*Melomys burtoni*) emerging from hiding during
403 open field tests from quoll-invaded sites in 2017 ($n = 16$), 2018 ($n = 28$) and 2019 ($n = 29$), and quoll-free sites
404 in 2017 ($n = 14$), 2018 ($n = 35$) and 2019 ($n = 24$) on Indian Island, Northern Territory, Australia.

405
406 *Effects of novel predator on seed harvesting and predator-scent aversion*

407 Although there was no interaction between melomys density and quoll presence ($t_{18} = -$
408 0.251, $P = 0.805$; Fig. 5), there was a very clear positive relationship between melomys
409 density and seed take ($t_{18} = 5.112, P < 0.001$; Fig. 5) and a clear negative relationship
410 between quoll presence and seed take ($t_{18} = -2.344, P = 0.031$; Fig. 5).



411

412

Figure 5. Effect of estimated population size on the number of control, unscented seeds removed from seed plots ($n = 21$) in quoll-invaded and quolls-free sites. Dotted lines denote the effect of quoll presence on seed removal rate.

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When we looked at the difference in seed take (Δ_{ks}) between scent treatments

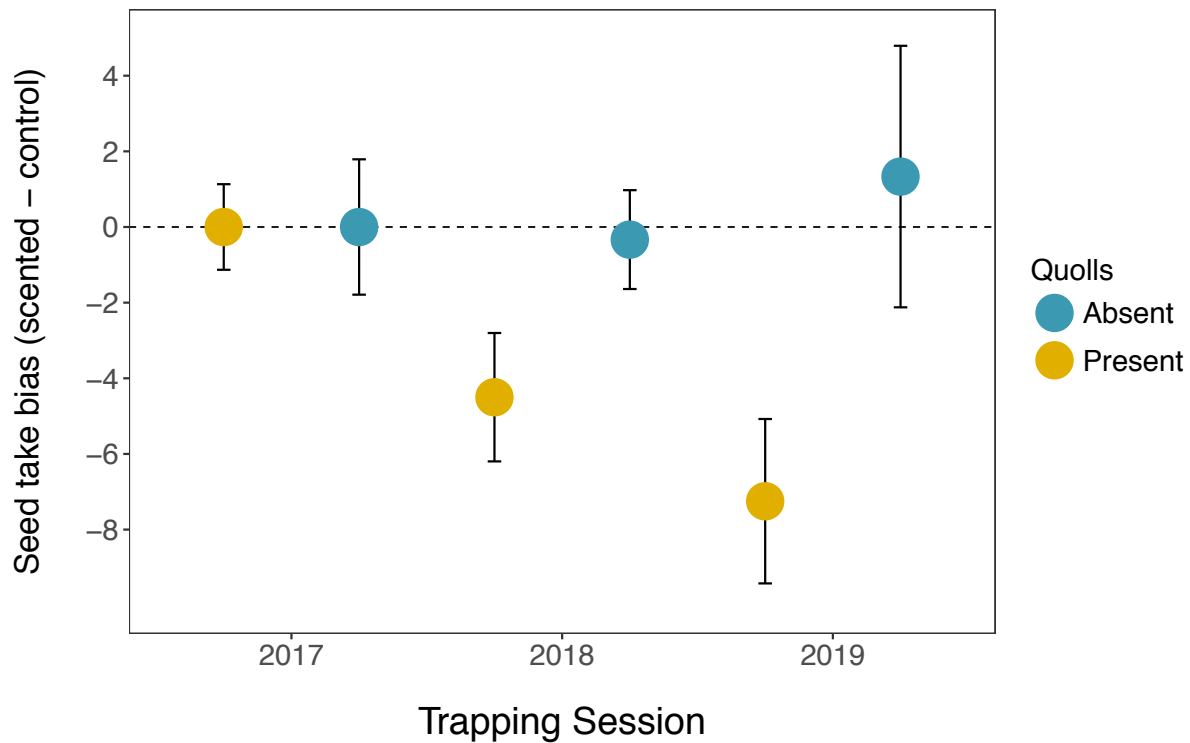
417

within site.session, a striking pattern emerges, in which there is a clear interaction between

418

the presence of quolls and session ($F_{3,17} = 18.61, P < 0.001$; Fig. 6).

419



420

421 **Figure 6.** Mean (\pm 95% CI) difference (Δ) between the number of predator-scented seeds and control,
422 unscented seeds removed by melomys from quoll-invaded ($n = 3$; 2017 & $n = 4$; 2018-19) and quoll-free ($n = 4$;
423 2017 & $n = 3$; 2018-19) sites during each trapping session.

424

425 **DISCUSSION**

426 The introduction of northern quolls to Indian Island was associated with lowered survival
427 and an apparent drop in population size in quoll-invaded melomys populations. This
428 numerical effect on melomys density had an impact on seed predation rates, because seed
429 take is strongly associated with the density of melomys in this system. This is a classic
430 trophic cascade: predation suppresses herbivore density, which reduces the pressure that
431 herbivores place on primary producers. Our study, however, also reveals an additional,
432 subtler, cascade effect; driven by altered prey behaviour rather than by altered prey
433 density.

434 Within months of quolls appearing on the island, invaded populations of melomys
435 were significantly shyer than nearby, predator-free populations of conspecifics. This rapid
436 but generalised response to a novel threat appears to have had a subtle effect on seed
437 predation rates: when we examine unscented seeds, per capita seed take is slightly lower in
438 quoll-invaded populations. This generalised response appears to have been supplemented
439 over time with more threat-specific antipredator behaviours. Although the willingness of
440 predator-exposed melomys to emerge from shelter (i.e. boldness) converged through time
441 with that of predator-free melomys, predator-exposed melomys continued to be more
442 neophobic than their predator-free conspecifics throughout the study. Meanwhile,
443 predator-scent aversion, as evidenced by seed plots, steadily increased over time.
444 Presumably the significant and novel predation pressure induced by the introduction of
445 quolls resulted in selection on behaviour and/or learning in impacted rodent populations,
446 allowing them to fine-tune their behavioural response (decrease general shyness, but
447 maintain neophobia, and respond to specific cues) as the nature of the threat became
448 clearer. These changing behavioural responses imply a generalised reduction in seed take
449 that also becomes fine-tuned over time, with high risk sites (those that smell of predators)
450 ultimately displaying substantially lower seed take than low risk sites. Thus, we see a
451 reduction in seed take resulting in a fine-scaled aversive response varying on a spatial scale
452 measured in the tens of metres.

453 Although our study documented dramatic population declines in predator-invaded
454 melomys populations, and we are assigning the causation of these declines to the
455 introduction of quolls, we need to address the confounding factors that may affect how we
456 interpret our results. Firstly, there is an inherent and unavoidable spatial confound in our
457 study system driven by the location of our study sites. We cannot exclude the possibility

458 that some of the population change we observe in our predator-invaded populations could
459 also be due to the population naturally declining towards sustainable levels unrelated to the
460 addition of a novel predator. It is possible that, by chance, when we started monitoring
461 populations of melomys, populations at northern sites were at a population peak and were
462 naturally cycling towards sustainable levels, while southern populations were stable.
463 However, although we cannot rule this out, such between population differences would be
464 expected to be driven by differences in resource availability between the locations (e.g.
465 Dickman *et al.* 1999; Russell & Ruffino 2012). We believe this is unlikely in our study system,
466 given the relatively close proximity of our sites (<10 km) and the spatially homogenous
467 climatic conditions that govern the wet-dry monsoonal tropics of northern Australia. Rodent
468 population cycles in the Australian wet-dry tropics appear to be primarily driven by annual
469 differences in rainfall between wet seasons, rather than spatial differences within years
470 (Madsen & Shine 1999). For this reason, we suspect natural population cycles are unlikely to
471 explain the population change differences we observe in this study.

472 Additionally, there is the unplanned, confounding factor of the fire that burnt
473 through northern Indian Island after completion of our population monitoring in 2017. Such
474 fires are commonplace in the Australian wet-dry tropics (Russell-Smith & Yates 2007); a
475 regular disturbance that is often rapidly offset by the annual monsoon driven wet season.
476 Since our sites are composed of grass-free woodland, the fire that burnt through them
477 mostly burnt leaf-litter (though it reached the mid-storey in other parts of the island). While
478 this likely reduced the short-term availability of food and cover for melomys, it is unlikely to
479 directly explain the demographic effects we observed. A previous study investigating the
480 effect of fire regimes on native mammals in savanna woodland in Kakadu National Park,
481 Northern Territory was unable to detect an effect of fire frequency or intensity on the

482 survival or recruitment of grassland melomys, despite finding fire impacts in all other co-
483 occurring native mammals studied (Griffiths & Brook 2015). Interestingly, even in a system
484 where fire is much more infrequent and significantly more intense (e.g. mesic habitats of
485 eastern Australia), grassland melomys were found to be relatively unaffected by a wildfire
486 that caused significant impacts to a co-occurring native rodent, and any demographic
487 impacts felt by melomys were entirely absent within months of the fire (Liedloff *et al.* 2018).
488 Additionally, the most dramatic behavioural difference (boldness and neophobia) between
489 quoll-invaded and quoll-free sites was observed immediately prior to the occurrence of the
490 fire (early August vs. mid-August 2017). For the behavioural changes we observed that were
491 potentially confounded by fire, such as predator-scent aversion, we would expect to see
492 these effects decreasing with time since fire if fire was driving this response, instead we see
493 the opposite trend. Finally, if food had become strongly limiting as a consequence of the
494 fire, we would expect to have observed an increase in seed take in the burned (quoll-
495 invaded) sites, instead we saw a decrease. For these reasons, we suspect the fire was
496 unlikely to be directly responsible for the demographic effects to melomys we observed,
497 and fire cannot in any way explain the response we observed to quoll-scented seeds. We,
498 therefore, believe our interpretation of these changes as being driven mostly by the
499 addition of a novel predator to the system is the most parsimonious and globally coherent
500 interpretation of the data.

501 Predation is a pervasive selective force in most natural systems, driving evolutionary
502 change in prey morphology, physiology, life history and behaviour. Unlike morphology and
503 physiology, however, the labile nature of behaviour makes it a particularly powerful trait for
504 rapid response in a changing world (Réale *et al.* 2007; Sih *et al.* 2010b; Dall & Griffith 2014).
505 Behavioural comparisons of wild populations exposed to differing predation regimes

506 provides some support for the prediction that reduced boldness would be selected for
507 under high predation scenarios (Åbjörnsson *et al.* 2004; Bell 2005; Brydges *et al.* 2008) and
508 that the appearance of novel predators can result in bold individuals becoming shy
509 (Niemelä *et al.* 2012), however, the opposite pattern of response can also occur (Brown *et*
510 *al.* 2005; Urban 2007) or behavioural phenotypes can be unrelated to predation regime
511 (Laurila 2000; Carlson & Langkilde 2014). Interestingly, a number of studies have
512 demonstrated that individuals from high-predation areas were quicker to emerge (Harris *et*
513 *al.* 2010) and were bolder and more aggressive (Bell & Sih 2007; Dingemanse *et al.* 2007)
514 than predator-naïve conspecifics. Although we found the opposite pattern to this
515 immediately following the arrival of a novel predator, by the second year after predator
516 introduction we found the boldness of melomys converging with that of predator-free
517 populations. Thus, it is clear that the behavioural composition of these populations are
518 dynamic, and it seems likely this dynamism (and perhaps the capacity of the prey species to
519 identify specific threats) may explain some of the variation between earlier studies.

520 Although boldness may change over time, neophobia, as a generalised adaptive
521 response to predation pressure, is now well supported across a number of studies (Crane *et*
522 *al.* 2019). Individuals living under high predation risk scenarios have been shown to typically
523 display generalized neophobia (Brown *et al.* 2015; Elvidge *et al.* 2016), and neophobia can
524 increase the survival of predator-naïve individuals in initial encounters with predators
525 (Ferrari *et al.* 2015; Crane *et al.* 2018). Certainly, in our study, predator-exposed melomys
526 were significantly more neophobic than their predator-free conspecifics; an effect
527 maintained throughout the study.

528 Despite reduced survival, significant population declines, and clear behavioural
529 changes in invaded populations, it is impossible to determine with certainty from our data

530 whether changes in the behaviour of predator-invaded melomys populations are the result
531 phenotypic plasticity (learning) or natural selection. The low between trapping session
532 survival of melomys in quoll-invaded populations means few individuals survive between
533 sessions, so natural selection is a possibility, and selection on these behavioural traits is
534 potentially very strong. Although behavioural changes in predator-invaded populations
535 have been documented in a few systems where predator introductions have been staged
536 and experimentally controlled (Lapiedra *et al.* 2018; Blumstein *et al.* 2019; Cunningham *et*
537 *al.* 2019; Pringle *et al.* 2019), elucidating whether these observed changes arise because of
538 behavioural plasticity or natural selection can be exceptionally difficult. Rapid behavioural
539 responses of vulnerable prey to recovered predators has been observed in a single prey
540 generation, presumably due to behavioural plasticity (Berger *et al.* 2001; Cunningham *et al.*
541 2019). Similarly, behavioural adjustments to an introduced predator have been observed as
542 a result of natural selection on advantageous behavioural traits (Lapiedra *et al.* 2018). In
543 this study, although we had measures of individual behaviour, our between session
544 recapture rates of these individuals was sufficiently low that we had no longitudinal data
545 on the behaviour of individuals to test whether individuals were altering their behaviour or
546 whether natural selection was resulting in population-level change. It thus remains possible
547 (and quite likely) that both mechanisms were in play.

548 Although northern quolls represent a novel predator to melomys on Indian Island,
549 the two species' shared evolutionary history on the northern Australian mainland may
550 provide some explanation as to why this staged introduction resulted in rapid, finely-tuned
551 behavioural adjustment in melomys, rather than extinction. Isolation from predators can
552 rapidly result in the loss of antipredator behaviours from a prey species' behavioural
553 repertoire (Blumstein & Daniel 2005; Jolly *et al.* 2018a), dramatically increasing an

554 individual's susceptibility to predation following the introduction of either predator or prey
555 (Carthey & Banks 2014; Jolly *et al.* 2018b). But such outcomes are not inevitable: length of
556 isolation, co-evolutionary history, degree of predator novelty, density-dependent effects,
557 population size, and pre-existing predator-prey associations (Berger *et al.* 2001; Blumstein
558 2006; Banks & Dickman 2007; Sih *et al.* 2010a; Carthey & Banks 2014) are all likely to be
559 hugely influential in determining whether an invaded population adjusts to the invader or
560 proceeds towards extinction. Recently, a conservation introduction of Tasmanian devils to
561 an island previously lacking them found that their possum prey rapidly adjusted their
562 foraging behaviour to accommodate this newly arrived predator (Cunningham *et al.* 2019).
563 Despite possums having lived on the island in isolation from devils since the 1950s,
564 presumably, their long evolutionary history together on mainland Tasmania had them
565 primed to respond to this predatory archetype (Sih *et al.* 2010a; Carthey & Banks 2014;
566 Cunningham *et al.* 2019). This shared evolutionary history is likely responsible for both
567 possums' and melomys' ability to rapidly mount appropriate antipredator responses to the
568 introduction of these predators. The predators are novel within an individual's lifetime, but
569 the individual's ancestors have encountered them before.

570 Although our results suggest that invaded melomys populations are beginning to
571 adjust to the presence of northern quolls as a novel predator on Indian Island, there has
572 been no sign of demographic recovery from the addition of this predation pressure on the
573 island. Data from our seed removal experiment clearly demonstrated that the function of
574 melomys as seed harvesters and dispersers scales with density. Trophic cascades resulting
575 from the addition and loss of predators from ecosystems has been observed in a number of
576 systems globally (Ripple *et al.* 2001; Terborgh *et al.* 2001; Estes *et al.* 2011), and the results
577 can profoundly shape entire systems. As the only rodent and the dominant granivore in this

578 system, while melomys populations may or may not go extinct as a result of quoll invasion,
579 their reduced abundance and weakened ability to harvest and disperse seeds may have yet
580 to be observed, longer-term consequences for the vegetation structure and ecosystem
581 function of Indian Island (McConkey & O’Farrill 2016). Currently, grass is a rare vegetation
582 feature on Indian island (though it is a dominant feature of savanna woodlands generally),
583 and this is quite possibly a result of the high density of melomys on this (previously)
584 predator-free island. The presence of quolls may well change that, as both numerical and
585 behaviour responses of melomys cascade down to the grass community.

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

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617

618 **Data availability**

619 The datasets generated and analysed during this study are available via zenodo.org and can
620 be accessed via <https://zenodo.org/record/3563421#.XwQZO5MzbOQ>

621

622

623 **Conflict of interest disclosure**

624 The authors of this article declare that they have no financial conflict of interest with the
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