



Educating the enemy: Harnessing learned avoidance behavior in wild predators to increase survival of reintroduced southern corroboree frogs

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Funding information

University of Wollongong, Grant/Award Number: VC's Fellowship; Australian Research Council, Linkage Program, Grant/Award Number: LP170100351

Abstract

After decades of near-complete extirpation, the yellow-and-black-striped Southern Corroboree Frog (*Pseudophryne corroboree*) is being reintroduced into field enclosures that exclude all but avian predators. The frog's long absence means avian attack risk to reintroduced individuals is unknown, so we asked: does corroboree frog coloration make them vulnerable to predators? First, using painted clay frog models and humans as proxy predators, we found that, surprisingly, striped models were as difficult to detect as control black models, and were far less detectable than yellow models. Second, to quantify attack probabilities, we deployed 2,304 models twice in the species' former range. Of our recovered models, 18% of the striped models were attacked by birds, suggesting they are a significant threat. In our second deployment, we saw a significant reduction in attacks on all model colors with only 10% of striped models attacked. If predators generalize their avoidance learning to real corroboree frogs, strategically timed model deployment near release sites may enhance the probability of survival of reintroduced frogs. Our study suggests that model deployment could be an effective low-cost technique to increase the survival of reintroduced prey species, including, but not limited to, those potentially conspicuous to their natural enemies.

KEYWORDS

alpine, antipredator, aposematism, Australian Alps, chytrid, clay models, conservation, reintroduction

1 | INTRODUCTION

The success of reintroduction programs can depend on the depth of scientific knowledge on species' natural history (Berger-Tal et al., 2011). Understanding predator–

prey dynamics and directly measuring the potential impact of predation on postrelease survival can therefore help optimize reintroductions (Armstrong & Seddon, 2008). Species' vulnerability to predation largely depends on the experience predators have with the profitability of

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potential prey in combination with the experience prey have in successfully avoiding their predators. Captive and/or isolated prey populations can lose protective traits that are maintained in their wild counterparts through natural selection (Jolly, Webb, & Phillips, 2018). For example, over just 13 generations, northern quolls (*Dasyurus hallucatus*) descended from populations on a predator-free island lost protective traits that their mainland counterparts retained (Jolly et al., 2018). Predator awareness can be reinstated using conditioning techniques with model predators (Griffin, Blumstein, & Evans, 2000). For example, captive-raised tammar wallabies (*Macropus eugenii*) that do not exhibit natural predator-avoidance behaviors can be successfully trained to avoid foxes (*Vulpes vulpes*) before release by exposing them to taxidermy foxes as model predators. Similar conditioning techniques have also been used on El Hierro giant lizards (*Gallotia simonyi*) who subsequently change their behavior when in the presence of cats and kestrels (Burunat-Pérez, Suárez-Rancel, & Molina-Borja, 2018). Yet, the outcome of training is not always successful. For example, similar training techniques have also been used on greater bilbies (*Macrotis lagotis*), but whether training enhances survival in the wild is currently equivocal (Moseby et al., 2011; Moseby, Cameron, & Crisp, 2012).

An alternative approach to manipulating predation rates in conservation strategies is to teach the predator population to avoid prey. In their classic experiment, Nicolaus, Cassel, Carlson, and Gustavson (1983) showed that crows (*Corvus brachyrhynchos*) can be taught to avoid colored eggs containing a toxin, and then generalize to avoid eggs of the same color in other locations. Learned avoidance conditioning has also been a successful technique for teaching some Australian native predators to avoid eating the invasive cane toad (*Bufo marinus*), whose chemical defense is highly toxic to many Australian species (Ujvari, Mun, et al., 2013; Ujvari, Oakwood, & Madsen, 2013). For example, survival of the northern quoll (*D. hallucatus*) is enhanced when individuals are trained to avoid eating cane toads by feeding them toad-flavored sausages laced with thiabendazole which induces nausea (Indigo, Smith, Webb, & Phillips, 2018). When the prey species is the focus of conservation, generating or enhancing learned avoidance in the wild predator population is a logical extension of the learned-aversion methods so far applied to conservation. Brightly colored prey species may be particularly susceptible to predators upon reintroduction, so teaching predators to avoid them warrants investigation as a powerful tool in their recovery program.

Understanding the role an imperilled species' coloration plays in protecting them from predation is an important aspect of their natural history that should be incorporated into conservation plans. Predators can be

deterred by prey via protective coloration, a broad term that includes camouflage (concealing) and aposematism (warning). Camouflage includes background matching (crypsis/disruptive coloration), and individuals appearing to be something they are not (masquerade; Ruxton, Sherratt, & Speed, 2004). The protective value of camouflage lies in predators either failing to detect prey, or detecting them but misclassifying prey as something inedible (Guilford & Dawkins, 1991; Skelhorn, Rowland, Speed, & Ruxton, 2010). Upon reintroduction, extirpated species that rely on camouflage may experience the same level of protection as their ancestors if the environment has not changed in a way that now renders them conspicuous. However, this may be less likely for animals with warning colors (one type of aposematism).

Aposematic animals that use coloration as their signal are often conspicuous and easy to detect (Mappes, Marples, & Endler, 2005), but the protective value of aposematism comes from predators coupling the signal with unprofitability. Often it is essential that predators learn to associate a signal with unprofitability through experience interacting with the prey, sometimes killing the prey in the process (Endler & Mappes, 2004). Extirpated aposematic species that require predator learning for effective protection face a challenge upon reintroduction; if they are conspicuous, they may be fatally attacked if the current generation of predators is naive to the meaning of their signal. Thus, reintroduced aposematic prey may experience high predation rates as predators learn to avoid them, potentially devastating conservation efforts. However, learned avoidance is not always required. Predators may have innate aversion to certain color patterns—like black and yellow stripes (Lindström, Alvtalo, Mappes, Riipli, & Vertanen, 1999)—and preferentially avoid them in a neophobic response (Exnerová et al., 2007; Mappes et al., 2005). In addition, avoidance can be socially learned as individual predators observe each other attempting to subdue prey (Thorogood, Kokko, & Mappes, 2018). Reintroduced aposematic prey may thus be protected without predators having to learn avoidance, or in other cases face high levels of predation as predators learn about the prey's unprofitability. Thus, the effect of coloration on prey vulnerability cannot be assumed and ought to be measured when possible.

The IUCN Global Amphibian Assessment identified 26 Australian frog species needing ex situ intervention (McFadden et al., 2013). Of these species, several exhibit striking coloration, including the black-and-yellow striped southern and Northern Corroboree Frogs (*Pseudophryne corroboree* and *P. pengellyi*, respectively). Their coloration and the ability of *Pseudophryne* sp. frogs' to both acquire toxins from their diet and generate them de novo (*Pseudophryne* sp., see below) has led to the widely held assumption that the corroboree frogs are aposematic, though

this hypothesis has not been formally tested. Both species are threatened, and the Southern Corroboree Frog is critically endangered. For 40 years, Southern Corroboree Frogs have experienced a catastrophic population decline due, primarily, to living in sympatry with a chytridiomycosis reservoir species (*Crinia signifera*; Hunter, Marantelli, et al., 2010; Hunter, Speare, et al., 2010; Scheele et al., 2017). Southern Corroboree Frogs are now functionally extinct (Brannelly, Roberts, Skerratt, & Berger, 2017). Only a small number of individuals remain in the wild at translocated and reintroduced sites (McFadden, personal communication). Their survival is dependent on ex situ breeding and reintroduction (Berger et al., 2016). Reintroduction enclosures exclude mammalian and reptilian predators, but do not exclude birds, primarily visual hunters that have tetrachromatic vision (full color vision including sensitivity in the ultraviolet; Bennett, Cuthill, & Norris, 1994; Hart, Partridge, Cuthill, & Bennett, 2000; Brannelly et al., 2015). So, does Southern Corroboree Frog coloration make them vulnerable to bird attack?

We aimed to understand predation risk faced by reintroduced Southern Corroboree Frogs through two experiments using clay models to quantify the probability that frogs are detected and attacked by birds. We chose clay models because (a) real frogs are highly valuable for conservation, and (b) naturally occurring predation events are seldom witnessed in nature (Noonan & Comeault, 2009). In all experiments we used black, yellow, and black-and-

yellow striped clay frog models. By including plain black and yellow models we controlled for the relative extremes of detectability, and the colors themselves influencing detectability and attack independent of the pattern.

The aim of the first experiment was to measure the detectability (sensu Guilford & Dawkins, 1991) of our three types of clay models (Endler, 1991; Guilford & Dawkins, 1991). When using clay models to measure predation rates in free-ranging wild predators, it is impossible to determine when models are detected but ignored by predators (Rößler, Pröhl, & Lötters, 2018). We thus used humans as a proxy for predators to measure detectability, as is commonplace in sensory ecology, because unlike wild bird predators humans can tell us when they see a model (Bergeron & Fuller, 2017; Mappes, Kokko, Ojala, & Lindström, 2014; Seddon, Tobias, Eaton, & Ödeen, 2010). Although human vision differs from bird vision in that we do not detect ultraviolet, Southern Corroboree Frogs do not reflect in the ultraviolet, so humans can see the complete reflectance of Corroboree Frog coloration (Figure 1, Umers, Silla, Bailey, Shaw, & Byrne, 2016). Our hypothesis was that the model types differed in their detectability. We predicted that (a) if stripes camouflage frogs, then striped models would be detected at a similar rate to black models, and (b) if stripes make frogs conspicuous, striped models would be detected at a similar rate to yellow models.

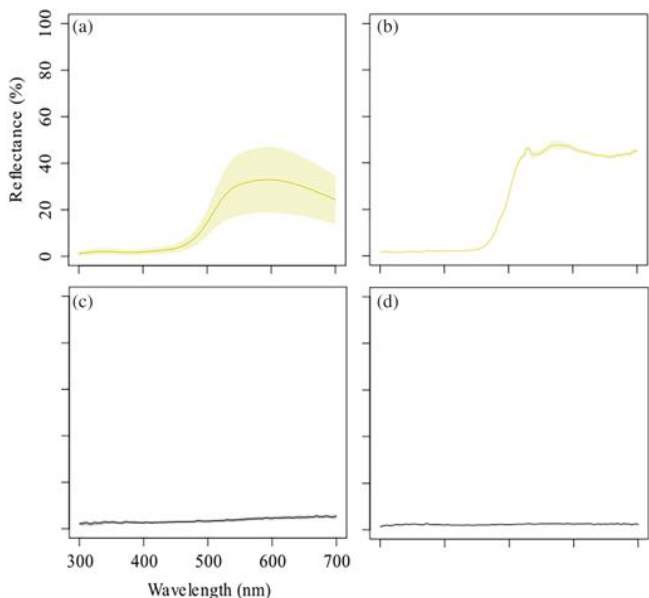


FIGURE 1 Reflectance of the yellow coloration of live Southern Corroboree Frogs (a), the yellow paint on our clay frog models (b), the black paint used on the black frog models (c), and the black stripes on the yellow-and-black striped frog models (d)

The aim of the second experiment was to understand how coloration influences the avian predation risk to reintroduced Southern Corroboree Frogs. We deployed clay models within parts of the Southern Corroboree Frog's former range and quantified avian attacks. Our hypothesis was that the model types differed in their probability of bird attack. We predicted that if corroboree frog coloration makes them vulnerable, and frogs are attacked by predators (because they have lost learned avoidance, lost innate avoidance, or never had innate avoidance), we would see similarly high attack rates on striped and yellow models, and low attacks on black models. However, if corroboree frog stripes are protective through concealing them from predators (camouflage), or if predators avoid their stripes, we expected similarly low attack rates on striped and black models, and higher attack rates on yellow models.

Finally, we aimed to determine whether the unprofitable experience of mistaking a clay model for food could deter predators in future encounters. We deployed our models a second time and tested for differences in attacks between the first and second deployments in the same locations 5 weeks apart. We predicted that predators would exhibit learned avoidance and be less likely to attack models in the second deployment after having had an initial unprofitable experience attacking a clay frog.

2 | METHODS

2.1 | Natural history

P. corroboree is a small toadlet endemic to alpine habitats above 1,200 m elevation in Australia with striking longitudinal black-and-yellow stripes (Figure 2). To people of the Wolgalu Aboriginal Nation the Southern Corroboree Frog

is known as Gyack (Connolly, Williams, & Williams, 2017). For Wolgalu people, Gyack's breeding calls herald preparation for travel to the Australian high country for important spring seasonal ceremonies and sacred business (Connolly et al., 2017). Corroboree frog breeding season is a signal of spring in the Australian Alps because it is triggered by the snow melt during which males gather in peat bogs to construct a small, dry chamber within vegetation and soil and call to attract females to mate. Females lay their eggs within the chamber, and the male remains inside it throughout the breeding season (January and February annually) (Byrne & Silla, 2017). Embryos develop within the egg until they reach an advanced stage, at which point they undergo diapause until winter rains stimulate hatching (Anstis, 2014). After hatching, tadpoles remain in winter pools and metamorphose in the following summer (about a year of development from egg deposition until metamorphosis) (Anstis, 2014). The frogs become sexually mature around 4 years old (Hunter, Osborne, Smith, & McDougall, 2009; McFadden et al., 2013). In general, *Pseudophryne* frogs possess defensive chemical compounds in the skin (Daly et al., 1990) derived both from their diet and de novo but it is unclear as to whether the corroboree frogs possess these toxins (Smith et al., 2002). Candidate avian predators in the frog's range probably include: Australian Magpie, *Cracticus tibicens*; Little Raven, *Corvus mellori*; Pied Currawong, *Strepera graculina*; and Laughing Kookaburra, *Dacelo novaeguinea*.

2.2 | Clay model approach and construction

The clay model experimental approach uses models to assess predation risk as an alternative to natural observation when predation is rarely observed, or individuals are

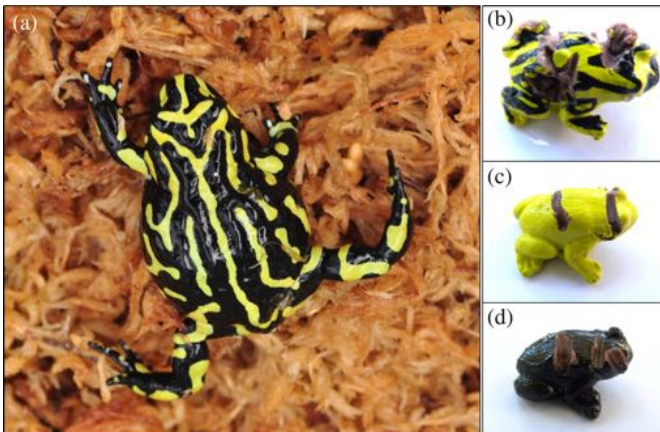


FIGURE 2 Photographs of (a) real Southern Corroboree Frog, and (b) black, (c) black-and-yellow striped, and (d) yellow frog models with bird attack impressions

rare. Our clay models were approximately 27 mm in snout-to-vent (SVL) length, comparable to a mature specimen of *P. corroboree* (25–33 mm SVL) (Anstis, 2014). To construct models, we heated clay and then poured it into silicone molds and allowed it to set. We used Monster Clay, which is an oil-based plasticine clay that sets firm but does not harden, ensuring the clay remains soft and can retain evidence of predation attempts (i.e., tooth or beak impressions). Three color patterns were selected for model coloration, “black,” “yellow,” and “striped” (Figure 2). Visual comparison with spectrophotometric measurements using a Jaz spectrophotometer (Ocean Optics, Dunedin) of live specimens of *P. corroboree* viewed at Taronga Zoo, and on eight individuals from a research colony at the University of Wollongong (see Umers et al., 2016), allowed for accurate color matching of paints used to color over the brown clay used to make all models (Figure 1). The black treatment ($N = 768$; black paint: Derivan Matisse “Raw Umber,” Series 1) had a dual function, controlling for the black stripes in the corroboree pattern and resembling a palatable, comparatively sized camouflaged species (e.g., *C. signifera*) found sympatrically with *P. corroboree*. The plain yellow treatment acted as a control for conspicuousness of the yellow in the corroboree frog pattern ($N = 768$; yellow paint: Resene “Bird Flower”). Black stripes were added to models painted with the same yellow as above to create the striped models ($N = 768$; yellow paint: Resene “Bird Flower”; black stripes: Black Uniball Posca PC-3M, Tokyo). Once the paint dried, clear acrylic gloss spray (MTN Montana Colors, Barcelona) was applied to all the models to give them a wet appearance, simulating the appearance of live frogs.

2.3 | Model detectability

We created a 10 m × 25 m grid of 30 models (10 per treatment) in a grassy field at the Hawkesbury Campus of Western Sydney University, similar to alpine sites where the models were deployed. Models were placed on both sides of a 1 m wide midline that spanned the 25 m length of the grid. Models were placed at intervals 1–5 m perpendicular to the midline on a wooden golf tee in the ground to stabilize them. Models were spaced haphazardly along the 25 m axis of the grid to ensure observers did not expect models at particular intervals. Before the trial, 34 observers were independently shown an unpainted model and were told that models similar to, but not the same as, the model they were shown could be found perpendicular to the midline between 1 and 5 m away. Landmarks were pointed out to observers to ensure boundaries of the grid were clear. Observers then followed an

experimenter that walked at a standardized pace (~1 m/s), and noted each model detected.

We used a generalized linear mixed effect model (GLMM using the *lme4* R package; Bates, Mächler, Bolker, & Walker, 2015) with a binomial distribution (*logit* link) to statistically analyze our data in R version 3.4.0 (R Core Team, 2017). We compared whether a model was detected (binary response variable: seen = 1, not seen = 0) between treatments (categorical fixed effect: black, yellow, or striped), while controlling for distance the model was from the pathway (continuous fixed effect) and differences between human subjects (random effect). Post hoc, to examine comparisons between all treatment types, we used the R function *lsmeans* from the *lsmeans* R package, and corrected *p*-values using Tukey’s HSD multiplicity adjustment (Lenth & Lenth, 2018).

2.4 | Model attacks

To assess attack rate by avian predators, we deployed 2,304 frog models (all three colors; $N = 768$ of each) on two separate occasions during the 2015/2016 summer in Kosciuszko National Park, New South Wales, Australia within the historic range of the Southern Corroboree Frog. Models were deployed first between December 28, 2015 and January 2, 2016 and, second, February 8–12, 2016. This was during the Southern Corroboree Frog’s breeding season when predators would most likely encounter adult frogs gathered together (Hunter et al., 2009). To measure changes in predator behavior, the same transects were used in both deployments. Transects were at four locations >2 km apart each containing 576 models. Transect starting locations were (a) 36°31′29.53″S, 148°15′50.31″E, (b) 36°24′21.81″S, 148°18′46.84″E, (c) 36°22′36.00″S, 148°22′12.00″E, and (d) 36°22′36.81″S, 148°29′1.31″E. These locations are more than 30 km from the nearest current Southern Corroboree Frog reintroduction site. To be clear, we are not providing location information on the current locations of Southern Corroboree Frogs (only our study’s transect locations) in order to keep the locations of this critically endangered species secret.

We deployed models in 24 rows of 24 frogs (8 models of each color in a randomized order 1 m apart) with each row approximately 100 m apart to maximize the likelihood of independent attacks (that different individual birds attack the models), which can be a common problem with clay model experiments (Noonan & Comeault, 2009) (Figure 3). We selected this “clumped” design because (a) as predator encounter rate increases, predators are more likely to learn when prey are clumped (Ender & Rojas, 2009; Gamberale & Tullberg, 1996; Riipi,

Alatalo, Lindström, & Mappes, 2001), and (b) because Southern Corroboree Frogs had a patchy distribution during their breeding season when they were abundant (Hunter et al., 2009). We pressed models onto golf tees to minimize the risk that they would be dislodged by forces other than predators (wind, rain, etc.). Models were not retrieved until after 96 hr in the field to avoid disturbing predators in the area while the models were present. We did not recover all the models that we deployed, as is the expectation in field-based model experiments of this magnitude (Table 1; Röbber et al., 2018). We excluded all missing models from our analysis because it is impossible to know the fate of the missing models, and because their missing status is not reliable evidence of predation (Röbber et al., 2018). Therefore, attack marks and subsequent statistical analyses were on recovered models only.

Following Low, Sam, McArthur, Posa, and Hochuli (2014), we categorized the attacks on recovered models as avian, mammalian, or unidentified. We attributed models showing deep U- or V-shaped marks to birds, whereas models exhibiting teeth impressions, such as incisor marks, were attributed to mammals (McElroy, 2016). Models that could not be confidently categorized by three independent observers were excluded from analysis ($N = 80$), and statistical analysis focused exclusively on avian attacks because they are motivated by visual cues, and because other predators are excluded from reintroduction enclosures.

We used G-tests to examine differences in the proportion of models recovered for each treatment. We used a GLMM with a binomial distribution (*logit* link; Bates et al., 2015) to statistically compare whether or not a model was attacked (binary response variable; attacked = 1, no attack = 0) between the first and second deployments. This model included the fixed effects of model treatment (categorical fixed effect: black, yellow, or striped), deployment (categorical fixed effect: first or second), and the interaction between these two variables.

It also included the random effect of location and row, to control for dependencies in our data due to the specific positions of deployment. We conducted post hoc comparisons between deployments and all treatment types using the same method as detailed in our analysis of the detectability study above (Lenth & Lenth, 2018).

3 | RESULTS

3.1 | Model detectability

Out of a possible 1,020 observations, our observers detected models 75 times (10 black, 3 striped, 62 yellow; Figure 4). Yellow models were more likely to be detected than black or striped models, and there was no difference in detectability between black and striped models (Table 2). As predicted by our GLMM, the mean probability of detection was 0.148 ($SE = 0.027$) for yellow models, 0.022 ($SE = 0.008$) for black models, and 0.006 ($SE = 0.004$) for striped models.

3.2 | Model attacks

3.2.1 | Comparing attacks between deployments

The proportion of models attacked by birds (of those recovered) was higher in the first deployment (21.7%, 314/1445) than the second (9.4%; 211/2236). As a proportion of recovered models for each treatment in the first deployment, birds attacked 27.9% (123/440) of black, 17.6% (86/489) of striped, and 20.3% (105/516) of yellow models (Figure 5). In the second deployment birds attacked 12.2% of black (88/723), 9.9% of striped (75/759), and 6.4% of yellow (48/754) recovered models (Figure 5).

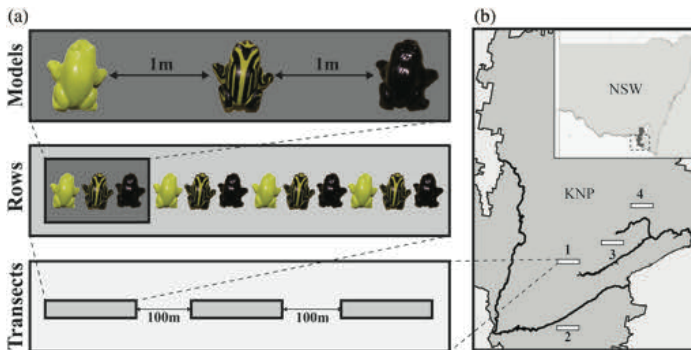


FIGURE 3 Experimental setup of each transect within Kosciuszko National Park (KNP), New South Wales (NSW), Australia. Models were placed 1 m apart separated into 24 per row, with 24 rows per transect that were separated by ~100 m

TABLE 1 A summary of 13, haphazardly chosen, clay model studies completed since 2000 to provide rough guidelines on the number of models and treatments typical for clay model design, and on which to base expectations of the percentage of models attacked. This is not intended to be a complete summary of all clay model studies. It is presented with the aim that it can put our study (Row 1) in context, as well as direct experimental design of future studies

Citation	Species	Treatments	Number of models deployed	Number of recovered models	Method for dealing with unrecovered models	Number of models attacked	Percentage of models attacked
Present study	Southern Corroboree Frog <i>Pseudophryne corroboree</i>	3	4,608	3,681	Excluded from analysis	525	14.3
McLean, Moussalli, and Stuart-Fox (2010)	Lake Eyre dragon <i>Ctenophorus maculosus</i>	4	2,800	2,400	Not reported	20	0.8
Richards-Zawacki, Yeager, and Bart (2013)	Strawberry poison frog <i>Oophaga pumilio</i>	4	1,600	<1,600	Excluded from analysis	202	12.6
Comeault and Noonan (2011)	Dyeing poison frog <i>Dendrobates tinctorius</i>	3	1,891	1,874	Excluded from analysis	49	2.6
Howe, Lövei, and Nachman (2009)	Cotton bollworm <i>Helicoverpa armigera</i>	1	1,802	Unclear	Unclear	Not reported	3.9
Stuart, Dappen, and Losin (2012)	Strawberry poison frog <i>Oophaga pumilio</i>	4	2,400	2,335	Excluded from analysis	108	5.0
Vignieri, Larson, and Hoekstra (2010)	Deer mice <i>Peromyscus</i> sp.	4	250	238	Excluded from analysis	28	8.5
Bittner (2003)	Common garter snake <i>Thamnophis sirtalis</i>	4	480	480	Not applicable	50	10.4
Noonan and Comeault (2009)	Dyeing poison frog <i>Dendrobates tinctorius</i>	3	1,260	1,260	Not applicable	139	11.0
Stuart-Fox, Moussalli, Marshall, and Owens (2003)	Tawny dragon and red-barred dragon <i>Ctenophorus decessii</i> and <i>C. vadrappa</i>	4	2,200	2,200	Not applicable	113	5.0
Saporito, Zuercher, Roberts, Gerow, and Donnelly (2007)	Strawberry poison frog <i>Oophaga pumilia</i>	4	800	776	Analyzed twice, assuming attacked and not attacked	99	12.4
Chouteau and Angers (2011)	Mimic poison frog <i>Ranitomeya imitator</i>	3	1,800	1,580	Excluded from analysis	229	14.5
Amézquita, Castro, Arias, González, and Esquivel (2013)	Harlequin poison frog <i>Oophaga histrionica</i>	4	800	679	Excluded from analysis	150	22.0
Watson, Roelke, Pasichnyk, and Cox (2012)	Juvenile skinks with blue tails (multiple species)	4	180	Unclear	Unclear	Not reported	70.6

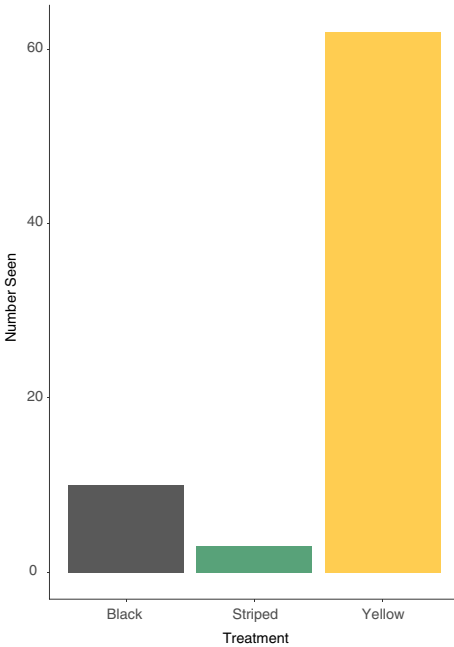


FIGURE 4 The number of models seen in each treatment by humans during our detectability experiment

TABLE 2 (a) Outcome of the generalized linear mixed effect model examining differences in the probability of detection by a human between model colors. Model estimates (β) of fixed effects presented are on the latent (*logit* link) scale with their corresponding *SEs*, variance estimates (σ^2) are supplied for residuals and random effects, and all significant values ($p < .05$) are presented in bold. (b) We also present comparisons of detection probability between all model colors, and in this case, *p*-values (p_{corr}) were corrected using Tukey's HSD multiplicity adjustment

(a) Output from the GLMM				
Variable names				
Fixed effects	β	<i>SE</i>	<i>z</i>	<i>p</i>
Intercept (black)	-2.786	0.430	-6.475	<.001
Treatment (striped)	-1.303	0.667	-1.954	.051
Treatment (yellow)	2.053	0.360	5.697	<.001
Distance	-0.327	0.094	-3.468	.001
Random effects	σ^2			
Observer	0.512			
Residuals	1.000			
(b) Multiple comparisons between model colors				
Model colors	β	<i>SE</i>	<i>t</i>	p_{corr}
Black vs. yellow	-2.053	0.360	-5.697	<.001
Striped vs. yellow	-3.356	0.603	-5.561	<.001
Black vs. striped	1.303	0.667	1.954	.124

For all model treatments there was a significant reduction in probability of attack between the first and second deployments (Table 3). As summarized from raw data, the reduction in proportion of models attacked relative to those recovered was 15.7% for black (Tukey HSD comparison: $\beta = 1.308$, $SE = 0.190$, $z = 6.898$, $p_{corr} < .001$), 7.7% for striped ($\beta = 0.501$, $SE = 0.204$, $z = 2.449$, $p_{corr} = .014$), and 13.9% for yellow models ($\beta = 1.344$, $SE = 0.214$, $z = 6.279$, $p_{corr} < .001$).

3.2.2 | Summary of attacks from the first deployment

From the first deployment, 1,445 (62.7%) models were recovered. The recovery rate of this deployment was likely affected by an unexpected rainstorm that occurred on the last day of our model deployment. However, the proportion of models recovered did not significantly differ among treatments (57.2% black, 67.2% yellow, and 63.6% striped models; $G_2 = 3.83$, $p = .15$). Of the recovered models, a total of 383 (26.5%) models were attacked, and the majority of attacks (82%) were from birds (4% mammals and 14% unknown). Bird attacks ($N = 314$, 21.7% of recovered models) were split between 123 (39.2%) on black, 105 (33.4%) on yellow, and 86 (27.4%) on striped models (Figure 5).

Within the first deployment the mean probability of attack, as predicted from our GLMM, was 0.220

($SE = 0.125$) for black, 0.104 ($SE = 0.068$) for yellow, and 0.088 ($SE = 0.059$) for striped models. The probability of bird attack was significantly higher for black models than yellow ($\beta = 0.887$, $SE = 0.181$, $z = 4.890$, $p_{corr} < .001$) and striped models ($\beta = 1.076$, $SE = 0.190$, $z = 5.667$, $p_{corr} < .001$; Figure 5). There was no difference in the probability of bird attack between yellow and striped models ($\beta = -0.188$, $SE = 0.186$, $z = -1.012$, $p_{corr} = .569$; Figure 5).

3.2.3 | Summary of attacks from the second deployment

Thirty-seven days later, we deployed a further 2,304 models. During this second deployment the weather was mild, and we recovered 2,236 models (97%). The proportion recovered did not significantly differ among colors ($G_2 = 0.52$, $p = .77$); we recovered 94% of black, 98% of yellow, and 99% of striped models. In total 239 (11%) models were attacked, and the majority of attacks (88%) were from birds (5% were from mammals and 7% were

unknown). Bird attacks ($N = 211$ or 9% of recovered models) were on 88 (41.7%) black, 75 (35.5%) striped, and 48 (22.8%) yellow models.

Within the second deployment the mean probability of attack, as predicted from our GLMM, was 0.071 ($SE = 0.048$) for black, 0.055 ($SE = 0.038$) for striped, and 0.029 ($SE = 0.021$) for yellow models. Probability of attack was not different between striped and black models ($\beta = 0.269$, $SE = 0.182$, $z = 1.480$, $p_{corr} = .301$), but was significantly higher for black ($\beta = 0.923$, $SE = 0.203$, $z = 4.551$, $p_{corr} < .001$) and striped ($\beta = 0.655$, $SE = 0.206$, $z = 3.181$, $p_{corr} = .004$) than yellow models (Figure 5).

4 | DISCUSSION

We aimed to understand the predation risk facing reintroduced Southern Corroboree Frogs and explore the application of clay model deployment as a conservation tool that exploits learned predator aversion to increase the likelihood of survival in reintroduced prey species. We

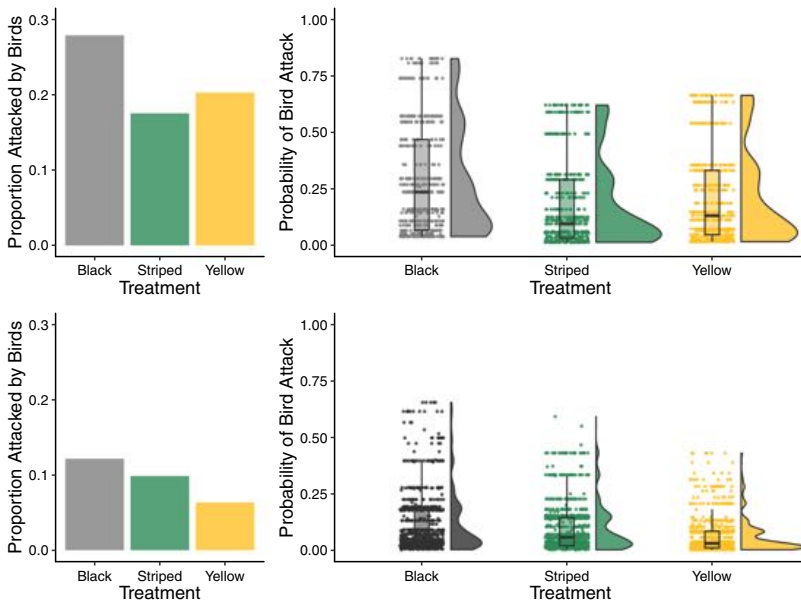


FIGURE 5 The proportion of recovered models that were attacked by birds (left panels), and the predicted probability of bird attack (right panels) for each model treatment from the first (top) and second deployments (bottom). The predicted probability of bird attack is depicted with a split violin plot, dot plot, and a simplified boxplot showing the mean and 95% confidence intervals. Lines connecting the model treatments with an asterisk above them indicate significant differences

Variable names	Model output			
	β	SE	z	p
Fixed effects				
Intercept (black, 1)	-1.263	0.727	-1.737	.082
Treatment (striped)	-1.076	0.190	-5.667	<.001
Treatment (yellow)	-0.887	0.181	-4.890	<.001
Deployment (2)	-1.308	0.190	-6.898	<.001
Treatment (striped): deployment (2)	0.807	0.263	3.067	.002
Treatment (yellow): deployment (2)	-0.036	0.271	-0.133	.894
Random effects	σ^2			
Row	1.007			
Location	1.868			
Residuals	1.000			

TABLE 3 Outcome of the generalized linear mixed effect model examining differences between deployments and model colors in the probability of bird attack. Model estimates (β) of fixed effects presented are on the latent (*logit* link) scale with their corresponding SEs, variance estimates (σ^2) are supplied for residuals and random effects, and all significant values ($p < .05$) are presented in bold. Post hoc multiple comparisons between model treatments across and between deployments can be found in the Results section

found that Southern Corroboree Frog black-and-yellow striped coloration does not make them conspicuous, but instead makes them as difficult to detect as black cryptic models (by humans). This suggests that from a distance at least, corroboree frogs are camouflaged by their stripes. We also found that although similar in detectability, striped models were less likely to be attacked than black models in the wild when avian predators first encountered them. Consistent with other clay model studies, the characteristic V- and U-shaped impressions on our models indicated that birds were the most common predators (Chouteau & Angers, 2011; Comeault & Noonan, 2011; Hegna, Saporito, & Donnelly, 2012; Rößler et al., 2018).

Birds attacked about 18% of striped models in our first deployment, and when we deployed the models a second time, around 5 weeks later, about 10% of striped models were attacked. Our interpretation of this result is that corroboree frog coloration has some protective value against avian predators, but that birds are still a significant threat if 1 in 5 reintroduced individuals are vulnerable to attack and that a reduction to a 1 in 10 chance of attack is a worthwhile improvement. A similar significant reduction in avian attack rate was seen in the other model colors, specifically 16% fewer black and 14% fewer yellow models were attacked in the second deployment. The drop in attack rates between deployments is consistent with aposematism theory, which posits that encounters with unprofitable prey—conspicuous or not—are efficiently learned and remembered and subsequently, similar prey are avoided in the future (Roper & Redston, 1987). Our results thus suggest that birds learned to avoid unprofitable clay models in repeat encounters (Dell'aglio, Stevens, & Jiggins, 2016). If birds generalize from models

to real frogs, it should be possible to condition birds to avoid real frogs based on a previous unprofitable experience with clay models.

4.1 | The disparity between detectability and attack rates for model types

The detectability of our frog models to humans did not match their likelihood of being attacked by birds in the first deployment. The first deployment in our study is most likely to represent the predator population's natural response to Southern Corroboree Frogs upon their reintroduction (i.e., their behavior without any prior interaction with our clay models). Black models were difficult for humans to detect, but, in the first deployment, the most likely to be attacked by birds. Striped models were also difficult for humans to detect, but had a lower probability of bird attack than black models. On the other hand, yellow models were highly detectable by humans, but were less likely to be attacked than black models.

It is impossible to know whether birds detected but ignored models, as opposed to not detecting them at all. Yet, if we assume that humans are suitable proxies for bird vision (given the lack of UV in the coloration of Southern Corroboree Frogs), then we can generate a few hypotheses for further testing: (a) the disparity between low detectability and relatively higher attack rates on black models may reflect bird preference for a similar-sized frog species sympatric to Southern Corroboree Frogs, the common eastern froglet (*C. signifera*); (b) the high detectability of yellow models, but subsequent low attack rate may suggest that yellow frogs were detected

but avoided, which may shed some light on why some frog species turn yellow in the breeding season (i.e., Lesueur's frog, *Ranoidea lesueuri*; Bell & Zamudio, 2012); and (c) if birds detect striped models as frequently as black models, that striped models are less likely to be attacked after detection than black models.

4.2 | The protective mechanism of Southern Corroboree Frog coloration

Striped and black models were similarly detectable to humans, and both these color patterns were less detectable than yellow models. During the first deployment, black models had a higher probability of bird attack than both striped and yellow models. Our data invoke two nonmutually exclusive hypotheses to explain the mechanism by which corroboree frog coloration influences predator behavior: (a) that the Southern Corroboree Frog color pattern may hinder predator detection by disruptive camouflage or (b) that birds may detect, but preferentially avoid the striped pattern on first encounter because innately they associate the coloration with unprofitability (i.e., aposematism) (Lindström et al., 1999; Mappes et al., 2005; Rojas, 2017). Future experiments should test whether the stripes have a deterring function at close distance, but a concealing effect at long distance (Tullberg, Merilaita, & Wiklund, 2005). Our detectability study suggests that at a long distance, to a human viewer, Southern Corroboree Frog coloration is camouflaging. Yet, we advise careful interpretation of our detection experiment results, and stress that they be viewed independently from the results of the field deployment. We present them as indirect evidence toward understanding how Southern Corroboree Frog coloration influences predator behavior. To definitively test detectability of Southern Corroboree Frog coloration, future studies should identify bird predators and train captive birds to indicate detection in experiments with real corroboree frogs. Given the critically endangered status of these frogs, this approach would need to take place using animals in captive colonies.

4.3 | Could seasonal changes have affected our results?

We cannot rule out that a time-in-season effect explains the difference in attacks between deployments. Perhaps, for example, predators avoid frogs later in the season because insects provide more palatable alternative prey (Mappes et al., 2014). However, this is unlikely to influence our results because insect prey is abundant from

November to April, and our entire study occurred in the middle of this period. Also, we cannot be sure that the same individual predators attacked models in both deployments, though overlap is likely because many local predator species have stable territories and small home ranges (i.e., 2 km² in Australian Magpies, *C. tibicen*). Finally, although unlikely, local avian predators may have experience with Southern Corroboree Frog coloration through traveling to areas where Southern Corroboree Frog (about 30 km away), or its sister species, Northern Corroboree Frog, still persist (about 200 km away). For example, Little Ravens travel great distances (>50 km per day; Whisson, Weston, & Shannon, 2015). Even if predators do have experience with corroboree frogs through the above mechanisms, or others like social learning (Thorogood et al., 2018), the reduction in attack rates in the second deployment suggests model decoys promote learned avoidance.

4.4 | Clay model deployment in species reintroduction and recovery plans

An important part of the Southern Corroboree Frog recovery plan is to consider the behavior of local predators and minimize the risk they pose during reintroduction (Moseby et al., 2011). Including model deployment as a predator aversion technique in the reintroduction program may enhance the success of Southern Corroboree Frogs reintroduction in the Australian Alps. Habitats are constantly in flux and when long-extirpated species are reintroduced they may encounter changes in the behavior, like the loss of aversive behaviors, or a seasonal change in demography of the predator population, like a higher proportion of naïve fledgling predators (Armstrong & Seddon, 2008; Mappes et al., 2005, 2014; Thorogood et al., 2018). Our data suggest that Southern Corroboree Frog coloration provides some protection against current local avian predators, but that birds still pose a risk worth mitigating. One such mitigation technique could include strategically timed deployment of clay models near reintroduction sites—we suggest timing the deployment so that it would train predators that are most likely to encounter real frogs, but not so similar in time to the release of reintroduced frogs as to attract predators to field enclosures (see below). Additionally, deployment of models with particularly distasteful substances may be considered to expedite predator avoidance learning, although, our study seems to suggest that unprofitable interactions with clay models alone is enough to deter predators (Rößler et al., 2018).

More generally, we suggest that clay models could also be used across the world in reintroductions of other

imperilled, potentially conspicuous prey species. There are two obvious applications. First, clay model studies can be used to understand how a reintroduced species' coloration affects their predation rate in the wild. This is important knowledge about the predation risk that precious individuals from breeding programs may face once reintroduced. Second, predator conditioning via clay model deployment could be used to reduce predation risk from visual predators. Other bright-colored frogs, like the Panamanian golden frog (*Atelopus zeteki*) and the red-banded poison frog (*Oophaga lehmanni*), that are currently under-going ex situ breeding programs, may be good candidates. We recommend a case-by-case approach in model and deployment design (for review see Rößler et al., 2018). Briefly, there are six main considerations:

1. *Number and design of models*—The number of models should be large enough to ensure predators encounter and attack a sufficient number. Most clay model experiments receive attacks on between 5 and 30% of recovered models (Table 1). Depending on the research question, the number of treatments should be as small as possible (commonly four; Table 1) to ensure statistical power. Inclusion of a negative control should be considered—which would comprise all the model materials in a nonvisually similar presentation to control for attacks driven by novelty or non-visual senses. Consideration should be made as to the addition of a distasteful compound to the models (such as quinine), which may expedite any learning but is a trade-off as an additional factor to account for in the experimental design. The size, shape, and colors used for making the models require close quantitative scrutiny to ensure they match those of the real animals.
2. *Proximity to the threatened populations*—In the absence of direct evidence about the effect of models on predator behavior, models should not initially be deployed close to the threatened population in case they attract predators to the area. However, understanding the natural history of possible predators is important (i.e., home range size, seasonal movement patterns, spatial ecology, etc.) because predators may be highly localized and any learned response to the clay could break down with distance (Comeault & Noonan, 2011).
3. *Deployment duration*—Models should be deployed for a period long enough to ensure a sufficient number of attacks are recorded. Some studies check models each day for attacks to determine when to retrieve models, yet this may affect the presence of predators within the study area. Models should therefore be deployed long enough to be detected but not checked too often.
4. *Deployment timing*—Seasonal timing should be considered. One aspect to consider is that it would be beneficial to minimize encounters with adverse weather events. In the case of protecting species set to be reintroduced, models should obviously be deployed before reintroduction. More subtly, though, it is important to consider the life cycle of the predator. For example, fledglings may pose a big threat to species every spring. Longitudinal clay model studies that are repeated throughout a target species' active season may be able to give insight into the diversity of predator species over time, however, as our data show, multiple deployments can also affect predator behavior. Regardless, longitudinal clay model studies could yield data that would be useful information for timing of deployments to afford protection for species.
5. *Human resources*—The main costs of this approach are in making and deploying the models. Clay model studies often aim to identify attacking predators, so models are made of soft clay. In this approach 3D printing is often not appropriate, so models are often made by pouring soft-set clay into molds and then painting them by hand. This process can be laborious. Placing the models in the field one-by-one and retrieving them is also laborious but unavoidable.
6. *Molecular techniques*—Recently molecular techniques have been applied to clay model studies to identify predators by sampling saliva from the clay model, extracting DNA, and using this to identify predator species (Rößler et al. unpublished data). While the addition of this approach would add time and cost, it may also provide novel and critical data about the predator species targeting prey species during reintroductions.

5 | CONCLUSION

Habitats are constantly in flux and long-extirpated species may encounter changes in predators when reintroduced (Armstrong & Seddon, 2008). Our data suggest that corroboree frog coloration provides some protection against current local avian predators, but that birds still pose a risk worth mitigating. Contrary to expectations for a black-and-yellow striped frog, our data suggest that corroboree frog coloration makes them difficult to detect. Perhaps they are camouflaged and toxic—or perhaps they are camouflaged at a distance, but the yellow and black coloration renders them aposematic when viewed up close (Rojas, 2017). Such hypotheses are for future work in sensory ecology. For applied conservation research, our findings suggest that a strategically timed and strategically placed deployment of clay models could

be an effective predator mitigation technique. Deployment of models with particularly distasteful substances may be considered to expedite predator avoidance learning. Application of this technique into reintroduction programs might enhance the success of corroboree frog reintroduction within the Australian Alps and could also be applied to imperilled prey animals globally.

ACKNOWLEDGMENTS

We thank J. O'Hanlon, S. Knox, M. Duncan, S. Samuel, M. Humphries, and F. Andrews for help with model construction, G. Bourke, T. Kahlke, J. Ryeland, and E. Drinkwater for assistance during fieldwork. Taronga Zoo for access to specimens for photos and J. Van Dyke, B. Rojas, and J. Mappes for manuscript reviews. We also thank all anonymous reviewers for their helpful suggestions on our earlier manuscript drafts. Data in KU's GitHub Repository. Study approved by University of Wollongong Animal Ethics Committee (permit 14/08), and NSW National Parks and Wildlife Service (License SL101674).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

K.D.L.U. and P.G.B. conceived the study, M.B.J.K., G.T.D., and K.D.L.U. constructed models, M.B.J.K., G.T.D., and J.P.L. conducted the field work in Kosciuszko, K.D.L.U. and J.L.R. conducted the field work in Sydney, M.B.J.K. wrote the first draft, J.L.R. and K.D.L.U. conducted the statistical analyses, and K.D.L.U., J.L.R., and P.G.B. honed the manuscript for publication with input from all authors.

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SUPPORTING INFORMATION

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

How to cite this article: Umbers KDL, Riley JL, Kelly MBJ, Taylor-Dalton G, Lawrence JP, Byrne PG. Educating the enemy: Harnessing learned avoidance behavior in wild predators to increase survival of reintroduced southern corroboree frogs. *Conservation Science and Practice*. 2020;2:e139. <https://doi.org/10.1111/csp2.139>