



1 **Abstract**

2 Despite the growing need to use conservation breeding and translocations in species' recovery,  
3 many attempts to reintroduce animals to the wild fail due to predation post-release. Released  
4 animals often lack appropriate behaviours for survival, including anti-predator responses. Anti-  
5 predator training—a method for encouraging animals to exhibit wariness and defensive  
6 responses to predators—has been used to help address this challenge with varying degrees of  
7 success. The efficacy of anti-predator training hinges on animals learning to recognize and  
8 respond to predators, but learning is rarely assessed, or interventions miss key experimental  
9 controls to document learning. An accurate measure of learning serves as a diagnostic tool for  
10 improving training if it otherwise fails to reduce predation. Here we present an experimental  
11 framework for designing anti-predator training that incorporates suitable controls to infer  
12 predator-specific learning and illustrate their use with the critically endangered Hawaiian crow,  
13 'alalā (*Corvus hawaiiensis*). We conducted anti-predator training within a conservation  
14 breeding facility to increase anti-predator behaviour towards a natural predator, the Hawaiian  
15 hawk, 'io (*Buteo solitaries*). In addition to running live-predator training trials, we included  
16 two control groups, aimed at determining if responses could otherwise be due to accumulated  
17 stress and agitation, or to generalized increases in fear of movement. We found that without  
18 these control groups we may have wrongly concluded that predator-specific learning occurred.  
19 Additionally, despite generations in human care that can erode anti-predator responses, 'alalā  
20 showed unexpectedly high levels of predatory wariness during baseline assessments. We  
21 discuss the implications of a learning-focused approach to training for managing endangered  
22 species that require improved behavioural competence for dealing with predatory threats, and  
23 the importance of understanding learning mechanisms in diagnosing behavioural problems.

24 **Keywords:** anti-predator learning, conservation behaviour, corvid, learning mechanisms, pre-  
25 release training, reintroduction biology

## 1 **Introduction**

2 Many conservation translocations—i.e. human-mediated relocations of wildlife to improve  
3 species' and habitat recovery—fail despite large commitments of resources (Hoffmann et al.,  
4 2010; Seddon et al., 2014). . Many translocation failures can be attributed to predation after  
5 release (Fischer & Lindenmayer, 2000; Moseby et al., 2011), yet the behavioural mechanisms  
6 leading to increased predation are infrequently acknowledged or addressed (Berger-Tal et al.,  
7 2020). Therefore conservation interventions that reduce behavioural vulnerability to predation  
8 have the potential to improve translocation outcomes widely (Berger-Tal et al., 2020).  
9 Deficiencies in released animals' anti-predator responses(Berger-Tal et al., 2020; Shier, 2016),  
10 are a likely contributor to post-release predation and subsequent translocation failure,  
11 especially when source populations have been free from predation pressure (Ross et al., 2019)..  
12 Just as other natural behaviours often erode in human care (Kraaijeveld-Smit et al., 2006;  
13 McPhee & Carlstead, 2010), predator-free environments foster prey naivety, which results in  
14 ineffective anti-predator behaviour (Cox & Lima 2006).

15         Anti-predator training—in which animals living in predator-free environments are  
16 provided opportunities to learn about predators—can be a useful tool to combat prey naivety  
17 across taxonomic groups (Griffin et al., 2000; Moehrenschrager & Lloyd, 2016; Shier &  
18 Owings, 2006; Teixeira & Young, 2014), but its efficacy in translocation contexts often goes  
19 untested (Greggor et al., 2019; Ross et al., 2019; Rowell, 2020). Accordingly, despite some  
20 successes (e.g., (Shier & Owings, 2006; van Heezik et al., 1999), training has often failed to  
21 adequately change anti-predator behaviour (Campbell & Snowdon, 2009; Jolly et al., 2020) or  
22 improve survival post-release (Moseby et al., 2012). Without being able to pinpoint where and  
23 why anti-predator training goes wrong, we lose the ability to address naivety and vulnerability  
24 to predators for translocated animals.

1           Anti-predator training requires manipulating animal learning. Many species naturally  
2 learn about predators during development, a process that is facilitated by experiencing a  
3 predatory cue (e.g., the sight, smell, or sound of a predator) alongside a conspecific signal of  
4 danger (e.g., an alarm call, scent, or evidence of attack) (Griffin et al., 2000). Some  
5 interventions expose animals to low levels of true predation to accurately replicate these cues  
6 and facilitate learning (e.g., (Moseby et al., 2016; Ross et al., 2019). However, losing animals  
7 to predators pre-release is often not practical when working with endangered species, with few  
8 release candidates, or due to welfare concerns. Therefore Training efforts often try to mimic  
9 the natural learning process, by pairing an aversive stimulus (e.g., a conspecific alarm cue or  
10 physical restraint) with a predator or replica (Shier & Owings, 2006; Teixeira & Young, 2014).  
11 Ideally, these presentations utilize classical conditioning learning mechanisms, allowing  
12 animals to rapidly remember the predator, not simply the context where they encountered it  
13 (Griffin et al., 2000). When successful, pre-release training enables animals to distinguish  
14 predatory threats from non-threatening stimuli in the environment and respond to actual  
15 predators in the wild, despite never having been directly attacked. Such learning is necessary  
16 for training to be effective, but measuring anti-predator learning over the course of training is  
17 not always straightforward.

18           A common framework for demonstrating learning compares behaviour before and after  
19 training between a trained and a control, un-trained group (Griffin et al., 2000). While this  
20 setup can successfully document changes to anti-predator behaviour over the course of training,  
21 it does not expose the root causes of behavioural change. Specifically, two cognitive  
22 mechanisms—sensitization and generalization—can falsely present as predator learning in  
23 trained groups if not adequately addressed with experimental controls, each of which may have  
24 different downstream effects for post-release survival. Sensitization occurs when animals  
25 become more responsive to repeated presentations of stimuli, and is especially likely after a

1 mildly aversive stimulus (Shettleworth, 2010). If animals cue into aspects of the training setup  
2 and anticipate danger, sensitization during repeatedly fear-inducing training sessions could  
3 drive apparent anti-predator behaviour during training, without target animals actually learning  
4 about the predator (e.g., (Mathis & Smith, 1993). Accordingly, sensitized animals would be  
5 unlikely to engage in anti-predator behaviour when encountering a predator outside of the  
6 training setup. Second, animals may not learn about the predator itself, but simply learn a  
7 generalized fear of animacy or animate stimuli in certain situations. While responding fearfully  
8 to a broad category of animate stimuli (including towards non-predators) may help with initial  
9 survival since predators would be avoided, animals can incur energy and resource costs if they  
10 consistently over-respond to false predatory threats (Carthey & Banks, 2014). In both cases,  
11 animals that show a heightened response after training may not express optimal anti-predator  
12 responses post-release. Therefore, by including experimental controls that offer repeated  
13 presentations of fearful (but not predatory) stimuli, and controls with non-fearful, animate  
14 stimuli, training designs can document true anti-predator learning, while ruling out  
15 sensitization and generalization. These additional controls help diagnose why apparently  
16 trained animals may not experience the survival or fitness benefits training is expected to  
17 provide. Additionally, it can give managers and researchers an opportunity to assess the  
18 efficacy of training prior to release, which could prevent unnecessary deaths if training methods  
19 can be adjusted to facilitate predator-specific learning that reduces vulnerability to predators  
20 post-release.

21 To illustrate the importance of these cognitive considerations, we tested the efficacy of  
22 anti-predator training with the critically endangered ‘alalā, or Hawaiian crow (*Corvus*  
23 *hawaiiensis*). ‘Alalā went extinct in the wild in 2002 and have been the subject of intensive  
24 reintroduction efforts since 2016. Previous attempts to re-establish the species faced many  
25 challenges, including predation by their natural predator, the ‘io (Hawaiian hawk, *Buteo*

1 *solitaries*) (U.S. Fish and Wildlife Service, 2009). Therefore future planning efforts  
2 incorporated the use anti-predator to improve the chances of survival (VanderWerf et al.,  
3 2013). We examined the efficacy of training in breeding facilities with ‘*alalā* that were not  
4 designated for imminent release, allowing us to evaluate methods with a larger, more robust  
5 sample. We measured the anti-predator responses of ‘*alalā* towards a predator model before  
6 and after a classical fear conditioning training, across birds that received one of three  
7 treatments: a live predator, a control fear stimulus (net), and a control animate object (live  
8 chicken). These learning-focused control treatments were designed to help identify  
9 sensitization (fear-inducing, non-predatory net) or generalization (non-fearful, animate  
10 chicken) to identify if factors other than anti-predator learning contribute to increases in anti-  
11 predator behaviour.

12 Our experiment was designed to differentiate among these alternative learning  
13 processes that all otherwise produce heightened anti-predator behaviour in the context of  
14 training. If the live predator group responded with greater anti-predator responses to the model  
15 in the evaluation trial than the other two groups, there would be strong evidence that the training  
16 produced predator-specific learning, and therefore may reduce the probability of predation if  
17 these birds were released. In contrast, if ‘*alalā* showed little increase in anti-predator behaviour  
18 in the live predator group, or showed increases across any other group, the question of training  
19 effectiveness would be more complex. If ‘*alalā* responded with greater anti-predator behaviour  
20 in all three groups, we would infer that training caused the birds to become sensitized to  
21 threatening/novel stimuli, instead of producing predator-specific learning. With this result we  
22 would predict that training offers little advantage in helping animals avoid predators since they  
23 did not learn to fear the predator itself. Meanwhile, if ‘*alalā* showed increases in anti-predator  
24 behaviour in the live predator and chicken groups only, we would conclude they acquired a  
25 learned fear response to general animacy. From a conservation management standpoint, this

1 last outcome, which would not show predator-specific learning, could still be beneficial,  
2 depending on the energetic or resource costs ‘alalā may incur by responding unnecessarily to  
3 harmless avian or other animate stimuli. However, there are clear advantages to developing  
4 anti-predator training programs that facilitate learning to fear and display appropriate anti-  
5 predator behaviour only to the predators, and not to other animate or inanimate objects that  
6 present no risk.

## 7 **Materials and Methods**

### 8 *Study species*

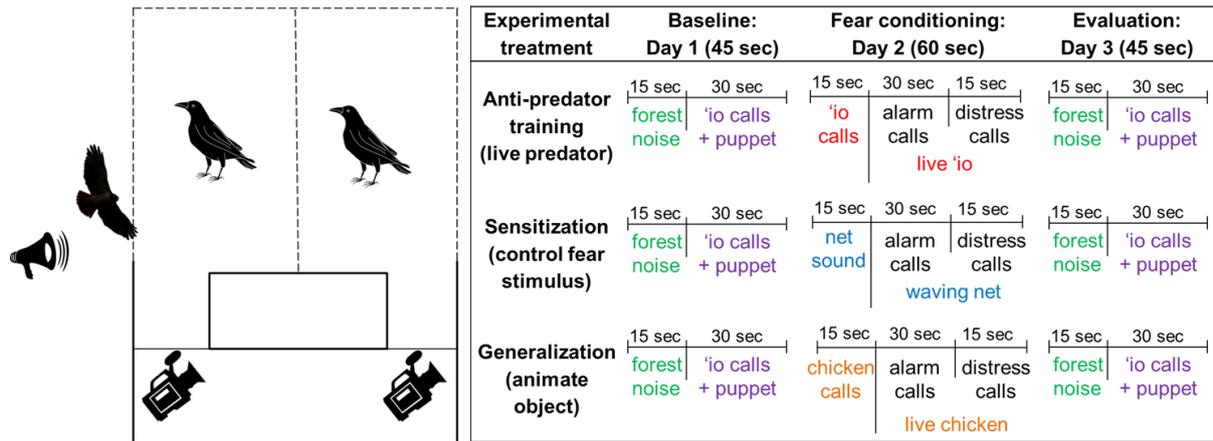
9 ‘Alalā are the only remaining corvid species native to the Hawaiian Islands. They are a  
10 generalist forager, with one surviving native predator, the ‘io. Populations of ‘alalā declined  
11 precipitously during the late 20<sup>th</sup> century due to habitat degradation, disease, human conflict  
12 and predation by non-native mammals (U.S. Fish and Wildlife Service, 2009). Despite  
13 supplementation translocations in the 1990’s, ‘alalā went extinct in the wild in 2002. Since  
14 then, conservation breeding has increased the population from fewer than 20, to over 120 in  
15 human care today. Reintroduction translocations were initiated in 2016 and are currently  
16 ongoing. However, translocation efforts have faced similar challenges over time. Predation by  
17 ‘io has been a primary cause of post-release losses in historical (U.S. Fish and Wildlife Service,  
18 2009) and ongoing translocations (Greggor et al., 2021). Therefore the development of anti-  
19 predator training to reduce mortality from ‘io figures prominently in recovery planning  
20 documents (VanderWerf et al., 2013). Despite the need for effective training, the small size of  
21 release cohorts and critically endangered status of the species meant that training for the release  
22 birds could not contain untrained control groups with later measures of survival, in case it  
23 resulted in the deaths of untrained birds (Greggor et al., 2021). Therefore, the need for further  
24 research arose within the conservation breeding flock, where control groups would not be

1 released and thus face no adverse survival impacts, to improve training methods in future  
2 recovery efforts.

### 3 *Birds and housing*

4 We tested ‘alalā housed in an ongoing conservation breeding program at the Keauhou  
5 Bird Conservation Center (KBCC) in Volcano, Hawai’i. Our sample comprised hand-reared  
6 (N=35) and partially or fully parent-reared birds (N=8). We tested ‘alalā in their home  
7 enclosures, with their mate, family group, or juvenile social group. Since ‘alalā are a social  
8 species, testing individuals alone can cause stress and compromise the reliability of anti-  
9 predator responses. Moreover, training is more effective in natural social groups (Shier &  
10 Owings, 2007). Therefore, data was taken on each individual within their group and the  
11 potential for social effects was accounted for statistically with mixed effects models (see  
12 below). No ‘alalā tested in this study had previously been trained to fear ‘io as part of release  
13 efforts, but all had the occasional opportunity to observe wild ‘io that are resident in the area.  
14 It is possible they may have observed predation events by ‘io on other forest birds, but these  
15 events were never observed by staff in the years leading up to this study.

16 All birds had access to food and water, and were exposed to ambient light and weather  
17 conditions. Each aviary contained areas of covered perching, an indoor feeding chamber, and  
18 open areas. See (Greggor et al., 2018) for a detailed description of husbandry, enrichment and  
19 housing practices. While the dimensions of each aviary differed slightly, the basic setup was  
20 the same (Fig. 1).



1

2 **Figure 1.** Experimental setup and schedule. In 13 of the 19 multi-chambered aviaries,  
 3 individuals could move freely between the two large chambers. The speaker (~2m from aviary  
 4 wall) and fear stimulus ('io pictured) were placed on the outside of the aviary. The behaviour  
 5 of birds was video recorded and observed live from inside the aviary's observation corridor.  
 6 The dotted lines indicate areas of mesh that offer visual access; areas without dotted lines are  
 7 solid walls through which the birds could not see. The experimenter presented the stimuli while  
 8 standing out of sight, up against the solid wall. During each trial, three minutes of behavioural  
 9 data was also taken immediately prior to and after the stimuli presentation listed above. The  
 10 fear conditioning day did not contain forest noise to prevent 'alalā from associating the forest  
 11 noise with the ensuing alarm and distress calls.

12

### 13 *Stimuli and trials*

14 We conducted all trials from July 7-20, 2018, between 08:00-16:00. We assigned each  
 15 aviary to one of three experimental treatments, exposing each bird group to a series of three  
 16 trials. The three trials (baseline, fear conditioning, and evaluation) occurred on consecutive  
 17 days at the same time of day. Each trial, regardless of treatment, consisted of three periods: 1)  
 18 a three-minute pre-trial observation, 2) a period of stimuli exposure (whose duration and  
 19 stimuli depended on the treatment and trial day), and 3) a three-minute post-trial observation  
 20 (Fig. 1). Including these pre- and post-trial periods for each trial allowed us to eliminate the  
 21 potential that we accidentally induced fear while setting up the trial, prior to the presentation  
 22 of stimuli, which would muddy the results. The experimenter set up the trials by putting out  
 23 the speaker and camcorders, allowing the birds to settle for ten minutes, and then beginning

1 the pre-trial observation period. The experimenter then presented experimental stimuli, which  
2 lasted either 45 seconds or one minute, depending on the trial type. Once the stimuli were  
3 removed, the three-minute post-stimuli period began. All trials followed this same schedule,  
4 but the stimuli differed by trial type and treatment group (Fig. 1).

5 We exposed each experimental group to the same stimuli for baseline (day 1) and  
6 evaluation (day 3) trials: an audio recording and a flapping model ‘io. These recordings  
7 contained 15 seconds of ambient forest noise (recorded at KBCC)—reducing the likelihood  
8 ‘alalā would be startled by a sudden sound from the speaker—followed by 30 seconds of ‘io  
9 territory calls. We created two exemplar audio recordings to address pseudoreplication, each  
10 with a similar number and timing of calls. Subjects randomly received one exemplar for the  
11 baseline and the other for the evaluation. During trials, the hidden experimenter presented the  
12 model ‘io next to the aviary as the recording started playing ‘io calls. The model was an ‘io  
13 taxidermy, mounted on a pole with wings extended, containing a mechanism that tipped the  
14 body forward on command. The experimenter moved the model similarly for each presentation,  
15 making the dipping motion every 2 seconds and holding for 2 seconds.

16 During fear conditioning trials (day 2) the experimenter presented one of three stimuli,  
17 depending on the experimental treatment: a live ‘io predator (anti-predator training), a net  
18 (sensitization control), or a live chicken (generalization control). The experimenter played  
19 sounds specific to the fear stimulus for 15 seconds, and then presented the stimulus alongside  
20 an audio track containing ‘alalā alarm and distress calls. We previously recorded ‘alalā alarm  
21 calls during husbandry-related disturbance (e.g., nest-checks) and distress calls during routine  
22 veterinary procedures. The alarm calls were overlaid on each other to mimic a flock of birds  
23 (increasing the perceived risk of danger, Coomes et al. 2019), followed by a single individual  
24 emitting a series of distress calls. Like other passerines, ‘alalā make distress calls when faced  
25 with imminent danger, such as during physical capture and restraint, potentially offering

1 information about threats to others (Griffin, 2008). No calls from experimental subjects in this  
2 study were used in the audio files.

3 For the live ‘io treatment we borrowed a glove-trained ‘io from the Panaewa Rainforest  
4 Zoo and Gardens in Hilo, Hawai’i. He was maintained at the KBCC in an outdoor enclosure  
5 between trials. He voluntarily stepped onto a falconer’s glove for each presentation and was  
6 encouraged to flap at the ‘alalā, in response to gentle motion of the glove. The handler remained  
7 hidden behind the side of the aviary, extending the glove into the area of visual access for the  
8 ‘alalā. The audio track used prior to the live ‘io presentation was a separate compilation of ‘io  
9 territorial calls than those used for baseline or evaluation trials.

10 For the sensitization control treatment, we presented a large black recapture net during  
11 the fear conditioning stimuli. As the primary recapture method at the facility, the net served as  
12 an artificial, fear-inducing stimulus. Before presenting the net, the experimenter clanked two  
13 net poles together repeatedly (every 2 seconds) for 15 seconds, simulating the sound of staff  
14 removing nets from work trucks during recapture. Immediately after the net sounds, the hidden  
15 experimenter played the ‘alalā alarm and distress calls, while waving the net in a similar range  
16 of movement to the ‘io’s flapping wings.

17 For the generalized animacy control treatment, we presented a live chicken during the  
18 fear conditioning trial. The ‘alalā had never seen a live adult chicken, and have no evolutionary  
19 history of predation by ground-based birds, so we predicted that it would not elicit anti-predator  
20 responses (although its novelty could still elicit neophobia, e.g., (Greggor et al., 2020). Prior to  
21 the presentation of the chicken, the experimenter played a series of non-fear related chicken  
22 calls. The hidden experimenter then played the ‘alalā alarm calls and held the chicken out on  
23 the side of the aviary, encouraging him to flap.

1 We edited sound files using Audacity® software and broadcast them from an Altec  
2 Lansing Bluetooth speaker. We broadcast sound files at the same maximum volume level (80  
3 dB), verified with the Decibel X Power Meter app for iPhones. Unless otherwise specified, we  
4 collected sound recordings using a Roland R-05 acoustic recorder and a Sennheiser  
5 microphone with a Rycote softie wind cover. Data collection and analysis

6 We collected behavioural data via live observer and video recorded from multiple  
7 angles. We recorded the number of anti-predator behaviours (alarm calls and rapid escape  
8 flights across the length of the aviary) and non-fear behaviours (affiliative begging calls) across  
9 each trial period (pre-stimuli, during stimuli, post-stimuli). Additionally, we classified birds'  
10 level of engagement with the stimuli into one of several categories (Table 1). An independent  
11 observer, blind to the experimental questions and original data, recoded a subset of videos  
12 (20%) to assess inter-observer reliability, which was calculated with an intraclass correlation  
13 coefficient (ICC).

14 **Table 1.** Definitions of behavioural categories used to explain levels of approach behaviour  
15 during exposure to the experimental stimuli.

| <i>Engagement level</i> | <i>Definition</i>  |
|-------------------------|--|
| Curiosity               | Bird makes a close approach (<2m) to the stimulus (or the point closest in their chamber to the stimulus) without any audible fear response  |
| Distant alarm calling   | Bird makes one or more alarm calls but does not approach the stimulus  |
| Mobbing                 | Bird alarm calls while approaching the stimulus <2 meters (or 2 meters of the closest point in their chamber to the stimulus). Can involve active aggression (hammering on enclosure) or persistent, close alarm calling |
| Vigilance only          | Bird makes no audible alarm response and no approach to the stimulus, but makes visible, alert changes to head position, such as sky-scanning or directing attention towards the stimuli                                 |

16

17 Non-fear behaviour occurred too infrequently (1.4% of trial periods) to merit formal  
18 analysis. Therefore, we focused on anti-predator behaviour and level of engagement with the

1 stimuli to answer three main questions. First, to confirm that all treatment groups began with  
2 similar levels of fear towards the 'io model, we compared anti-predator behaviours across  
3 treatments on the baseline trial (day 1). Second, to determine if the live predator, net, and  
4 chicken stimuli elicited different responses during the fear-conditioning trial, we compared  
5 anti-predator behaviour and engagement levels across treatments during fear conditioning (day  
6 2). Finally, we compared changes between baseline trials (day 1) and evaluation trials (day 3)  
7 across treatments to determine if anti-predator behaviour increased over trials to indicate  
8 predator-specific learning.

9         We compared anti-predator behaviour for each question with a generalized linear mixed  
10 model (GLMM) in R version 3.6.2 (Team, 2019) with the lme4 package (Bates et al., 2013).  
11 Each model contained the following explanatory variables: sex, number of birds present in the  
12 aviary, whether the bird had access to the stimuli side of the aviary, trial period (pre-stimuli,  
13 stimulus, post-stimuli), and treatment (anti-predator training, sensitization control and  
14 generalization control). Models examining changes to anti-predator behaviour over time also  
15 contained an interaction between trial number (baseline = 1, evaluation = 3) and treatment.  
16 Subject ID was included as a random factor for all models. Accounting for this source of non-  
17 independence was necessary since each individual contributed data points for the three trial  
18 periods, across all three trials. Age was not included since only one aviary contained birds  
19 younger than breeding age, and their data were not outliers. Parent- versus hand-reared birds  
20 were approximately evenly spread across treatments, and later inclusion of rearing type did not  
21 improve any final models, so this distinction was not included in main analyses (Table S4).  
22 The relative influence of factors was assessed with AICc values (calculated with the MuMIn  
23 package, (Barton, 2020) due to the relatively small sample size, and factors were dropped from  
24 the model if their inclusion did not reduce AICc values by >2. Model fit and assumptions,

1 including dispersion, outliers, uniformity and zero inflation were checked with the DHARMA  
2 package (Hartig, 2021), and data transformations and model error structure chosen accordingly.

3 We transformed anti-predator behaviours to a binomial variable (presence of anti-  
4 predator behaviour = 1, absence = 0) for comparing baseline responses across treatments. In  
5 analysing behaviour across treatments during the fear conditioning trial, we converted  
6 behavioural sums (alarm calls plus full flights) to a count per three-minute period, to account  
7 for the different trial period durations, and analysed them with a negative binomial error  
8 distribution. For the third question evaluating changes in anti-predator behaviour from the  
9 baseline to evaluation trials, we focused on the “during” stimuli period. We converted anti-  
10 predator behaviour to a count per three-minute period, square-root transformed it and analysed  
11 it with a Gaussian error distribution. We conducted a post-hoc power analysis on the GLMM  
12 for the during-stimuli comparison of baseline and evaluation trials using the simr package  
13 (Green & Macleod, 2016).

14 We conducted separate analyses to investigate birds’ engagement levels with the fear  
15 stimuli. We examined whether birds were more likely to respond within a certain category  
16 (Table 1) in the fear-conditioning trial (day 2) with an exact multinomial test, assuming an  
17 equal 25% chance of any behaviour occurring. We ran post hoc binomial tests with Bonferroni  
18 corrections to investigate categories of interest. We also compared birds’ response between  
19 baseline and evaluation trials with a marginal homogeneity test, using the coin package (Zeileis  
20 et al., 2008).

### 21 *Ethical statement*

22 This work using animal subjects was approved by San Diego Zoo Wildlife Alliance’s IACUC  
23 committee (No. 16-009). Permits allowed conservation breeding of ‘alalā (USFWS Native  
24 Endangered Species Recovery Permit TE060179-5, State of Hawaii Protected Wildlife Permit

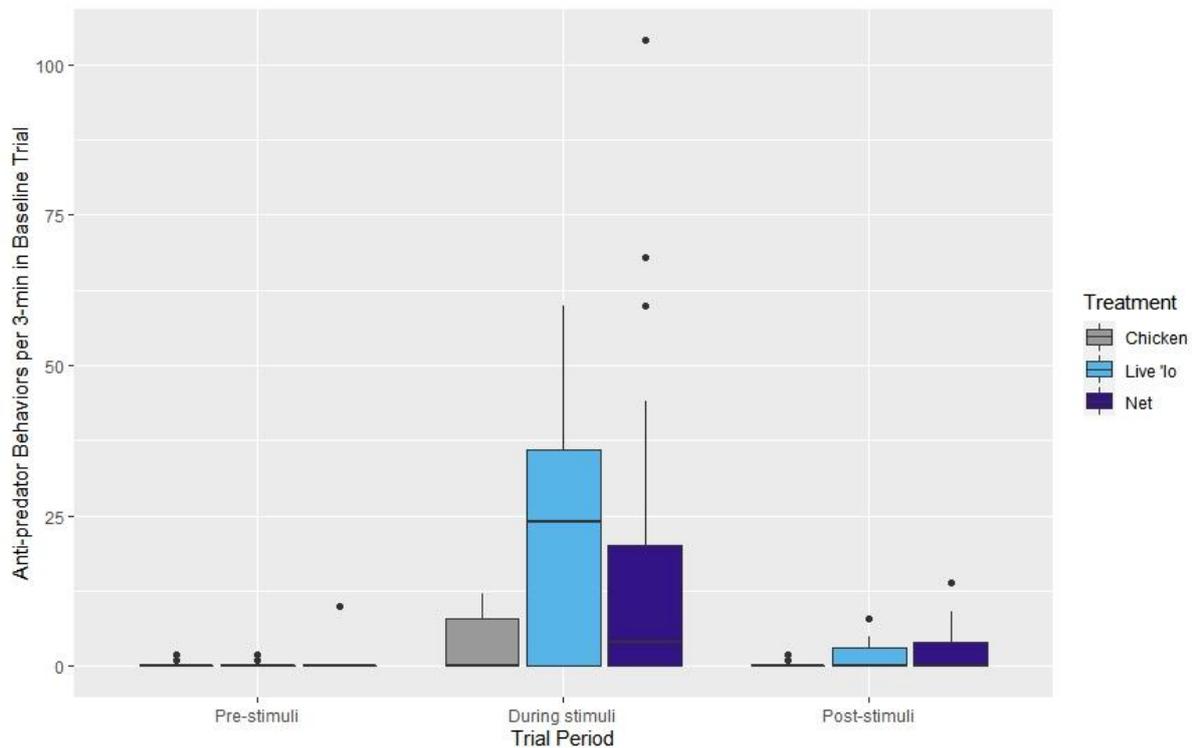
1 WL19-16) and the possession of live ‘io (USFWS Special Purpose Miscellaneous permit  
2 MB09204C-1).

### 3 **Results**

4 We tested 43 ‘alalā (N=13 chicken, 13 live predator, 17 net) across 19 aviaries. Of these, two  
5 aviaries were excluded for fear conditioning and evaluation trials (days 2 and 3) because birds  
6 in one aviary started breeding (net treatment), and in another the speaker malfunctioned  
7 midway through the alarm and distress calls (chicken treatment). Inter-observer reliability was  
8 high for the composite measure of alarm calls and full flights (ICC(1)=0.91,  $p < 0.001$ , CI=0.86-  
9 0.94), and for the level of engagement (96.4% concurrence). One bird was not reliably visible  
10 on video during the fear conditioning trial (day 2), and her data was removed for that day.

#### 11 *Treatment effect during baseline trials*

12 In baseline trials (day 1), all treatment groups showed increased anti-predator during the ‘io  
13 model presentation and post-stimuli time periods in comparison to pre-stimuli anti-predator  
14 rates (Binomial GLMM, N=129 observations, 43 birds across 3 periods; During:  $B=2.35 \pm 0.67$ ,  
15  $z=3.49$ ; Post-stimuli:  $B=1.46 \pm 0.62$ ,  $z=2.34$ ,  $\Delta AIC_c = -10.428$  relative to final model excluding  
16 this term; Fig. 2). Birds tested in larger social groups had slightly higher levels of anti-predator  
17 responses ( $B=0.87 \pm 0.43$ ,  $z=2.02$ ,  $\Delta AIC_c = -2.21$ ). There was no effect of treatment, as  
18 expected, since all groups were exposed to the same stimuli. Also, we found no effect of sex  
19 or bird access to the stimuli side of the aviary (Table S1).



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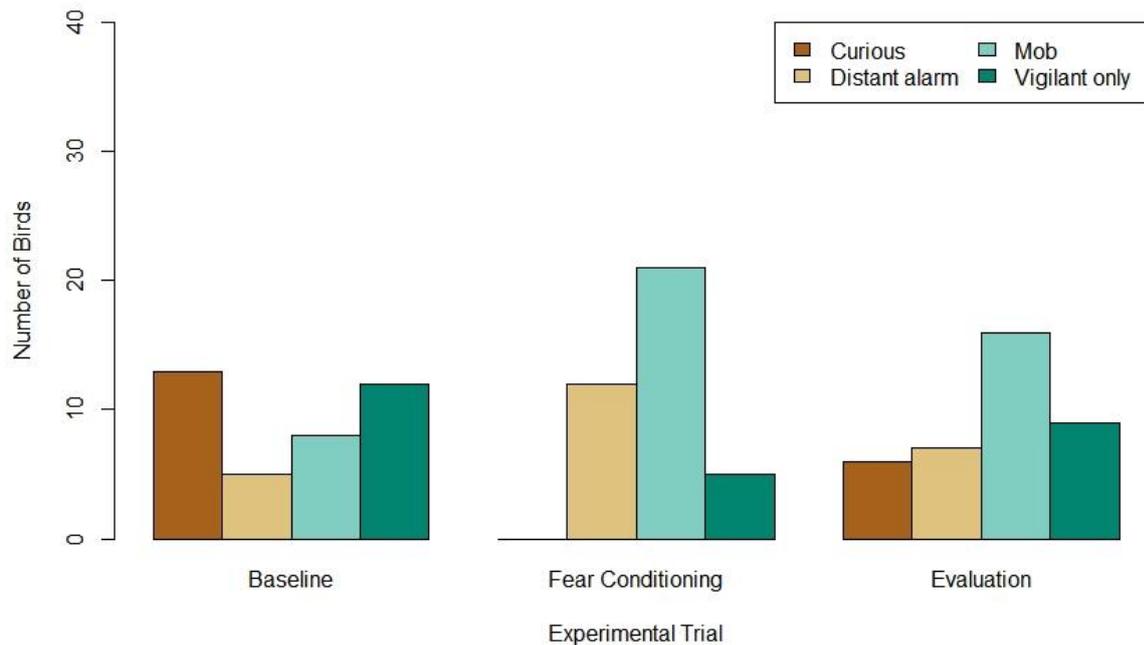
2 **Figure 2.** Boxplots depicting raw rates of individual anti-predator behaviour across trial  
3 periods of baseline trials (day 1). Outlying data points are pictured and horizontal line in each  
4 box depicts the median value. Anti-predator behaviour is measured as the rate of alarm calls  
5 and pace flies per minute of trial period. All treatments received the same stimuli during these  
6 baseline trials: a three-minute pre-stimuli period, 45 seconds of exposure to an 'io model and  
7 'io calls, and a three-minute post-stimuli period. There was no effect of experimental treatment  
8 and all conditions show the same pattern: little anti-predator behaviour during the pre-trial,  
9 increased fear while the model and calls were present, and reduced fear once stimuli were  
10 removed in the post-trial period.

11

### 12 *Treatment effect during fear-conditioning trials*

13 Similar to baseline trials, during the fear conditioning trials (day 2) 'alalā displayed higher rates  
14 of anti-predator behaviour during the stimuli presentation and post-stimuli period (GLMM,  
15 N=111 observations, 37 birds across 3 periods, During:  $B=3.82\pm0.16$ ,  $z=23.98$ ; Post-stimuli:  
16  $B=2.13\pm0.16$ ,  $z=12.79$ ,  $\Delta AICc=-2737.30$ ) relative to the pre-stimuli period. All treatment  
17 groups were indistinguishable in their rates of anti-predator behaviour, despite receiving either  
18 a live predator, net, or live chicken. However, birds in larger social groups had slightly higher

1 rates of anti-predator behaviour ( $B=0.69\pm 0.31$ ,  $z=2.55$ ,  $\Delta AICc=-2.61$ ). There was no effect of  
2 sex (Table S2). Additionally, while stimuli were present, ‘*alalā* were more likely to mob  
3 (Binomial test, Bonferroni correction applied,  $p<0.001$ ) and less likely to exhibit curiosity  
4 ( $p<0.001$ ; Figure 3).



5  
6 **Figure 3.** Number of ‘*alalā* exhibiting response categories to the stimuli during each trial  
7 type. During the Fear Conditioning trials, birds were more likely than chance to mob and less  
8 likely than chance to show a curious response. In comparing between trial types, more ‘*alalā*  
9 mobbed the taxidermy ‘*io* model during the Evaluation than Baseline trials.

10

### 11 *Treatment effect on predator-specific learning (baseline versus evaluation)*

12 There was no interaction between treatment and trial (Table 2). Across all treatments,  
13 ‘*alalā* increased their anti-predator behaviour towards the ‘*io* model during the evaluation trials,  
14 relative to baseline trials ( $B=1.51\pm 0.58$ ,  $z=2.62$ ,  $\Delta AICc=-4.87$ ; Figure 4). ‘*Alalā* tested in larger  
15 group sizes showed higher levels of anti-predator behaviour ( $B=1.95\pm 0.62$ ,  $z=3.13$ ,  $\Delta AICc=-$   
16 7.48). Additionally, more ‘*alalā* mobbed the ‘*io* model during evaluation than baseline trials

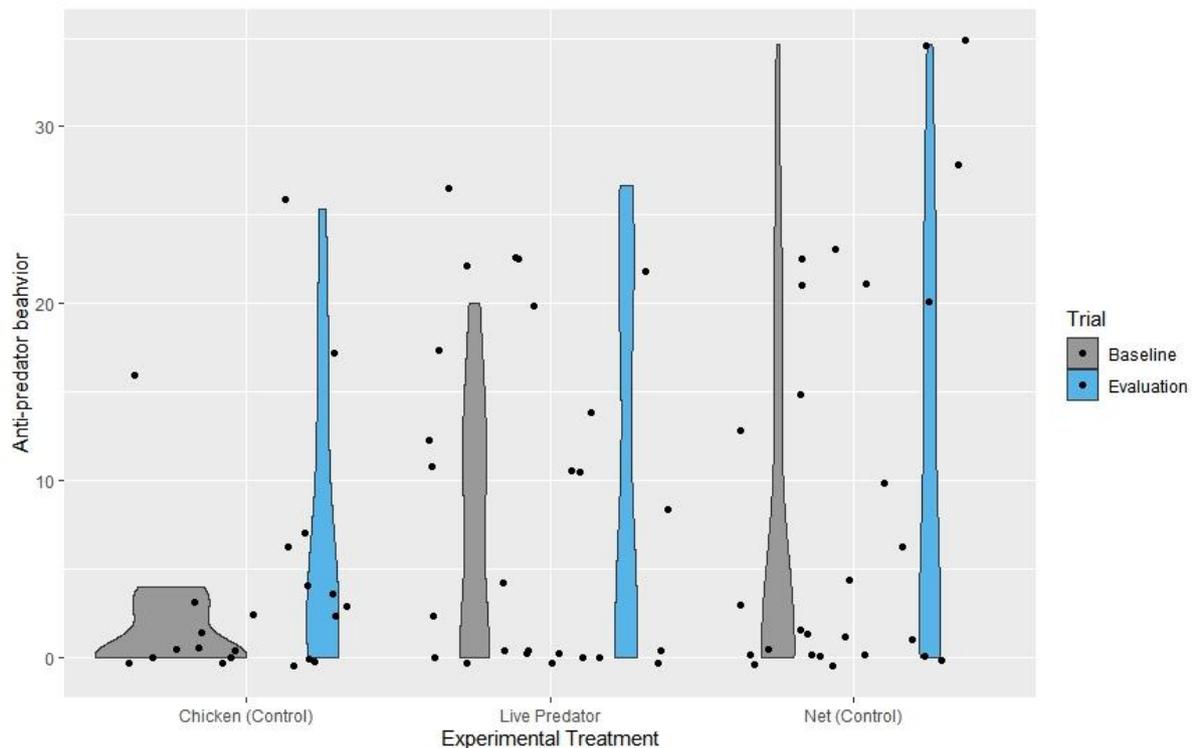
1 (Marginal Homogeneity test;  $\chi^2=8.027$ ,  $df=3$ ,  $p=0.045$ ; Figure 3). Power analyses revealed a  
 2 low likelihood of finding an effect during the stimuli presentations, even for relatively large  
 3 effect sizes, ( $B=4.0$ , power=62.90%, CI=59.82-65.90%;  $B=2.0$ , power=23.20%, CI=20.62-  
 4 25.94%;  $B=1.0$ , power=7.20% CI=5.68-8.98%). However, the data illustrate similar upward  
 5 trends from baseline to evaluation in each treatment group (Fig. 4), showing little support for  
 6 an interaction between treatment and trial, which would have indicated predator-specific  
 7 learning.

8 **Table 2.** Results of model selection process for GLMM on anti-predator behaviour during the  
 9 presentation of the 'io model with data from the baseline and evaluation Trial (day 1 and 3).  
 10 The experimental Treatment denoted groups that experienced either a live 'io, net or live  
 11 chicken. The model term Access denoted whether birds were housed in the chamber adjacent  
 12 to the experimental stimuli.

13 <sup>a</sup>The change in AICc represents the difference in AICc value from the model listed directly  
 14 above. Terms were included in the model if dropping them increased AICc by more than 2.

15 <sup>b</sup>Final model.

| <i>Model</i>   | $\Delta AICc^a$ |
|--|-----------------|
| Anti-predator behaviour ~ Num_birds + Trial + Treatment + Access + Sex Treatment + Treatment: Trial + (1 Bird) | 0.0             |
| Anti-predator behaviour ~ Num_birds + Trial + Treatment + Access + Sex Treatment + (1 Bird)                    | -2.49           |
| Anti-predator behaviour ~ Num_birds + Trial + Treatment + Access + (1 Bird)                                    | -1.38           |
| <sup>b</sup> Anti-predator behaviour ~ Num_birds + Trial + Treatment + (1 Bird)                                | -2.11           |
| Anti-predator behaviour ~ Trial + (1 Bird)   | +6.10           |
| Anti-predator behaviour ~ Num_birds + (1 Bird)   | +3.48           |



1

2 **Figure 4.** Violin plots and jittered raw datapoints depicting anti-predator behaviour on the  
3 baseline (day 1) and evaluation (day 3) trials across experimental treatments, while stimuli  
4 were present. Anti-predator behaviour is depicted here as the number of alarm calls and full  
5 aviary flights during the stimuli period. Birds in all experimental conditions demonstrated an  
6 increase in anti-predator behaviour during the evaluation in comparison to baseline trials, and  
7 no interaction effect was detected statistically.

8

## 9 **Discussion**

10 We illustrated a learning-focused approach to testing anti-predator training,  
11 incorporating suitable controls to determine whether predator-specific learning occurred. Using  
12 this approach, we measured the efficacy of training for increasing anti-predator behaviour in  
13 ‘alalā towards their natural predator. While we documented increases in anti-predator  
14 behaviours after training, our control treatments also saw increases, suggesting that factors  
15 other than anti-predator learning were in play. Also, we found that ‘alalā already showed  
16 substantial anti-predator wariness towards ‘io prior to experiencing training, and that birds  
17 displayed more anti-predator behaviour when tested in larger groups. Our results demonstrate

1 the difficulties in designing anti-predator training and emphasize the importance of considering  
2 alternative cognitive mechanisms underlying anti-predator behaviour.

3 Had we not conducted multiple learning controls, we may have wrongly concluded that  
4 predator-specific learning occurred in ‘alalā exposed to live predator training. Many published  
5 accounts of training include only a non-training control to support their efficacy (Crane &  
6 Mathis, 2011; Teixeira & Young, 2014). Yet, we have shown that several alternative cognitive  
7 hypotheses could explain a similar increase in fear after exposure to training and control  
8 stimuli. ‘Alalā displayed more anti-predator behaviour toward an ‘io model after the live  
9 predator and either control treatment, suggesting that they became sensitized to the setup and  
10 anticipated the appearance of dangerous stimuli. In other words, the initial model ‘io may have  
11 primed the birds to find the next presentation of the model scarier than before (the opposite of  
12 habituation, (Shettleworth, 2010). Alternatively, experiencing multiple days of fear stimuli  
13 may have put the birds in a sustained agitated state (e.g., (McIvor et al., 2018), causing them  
14 to react more strongly to the predator model over time. In future, work with ‘alalā and other  
15 species being trained for reintroduction could extend the time between baseline and evaluation  
16 trials or conduct the evaluation trials in a different enclosure (e.g., (Mathis & Smith, 1993),  
17 potentially reducing the likelihood that animals carry over motivational effects between trials.  
18 This would remove one potential source of sensitization, and also reduce the likelihood that  
19 other non-learning factors, such as neophobia, contribute to anti-predator responses (Abudayah  
20 & Mathis, 2016).

21 We faced a challenge that is common to many translocation programs; there are often  
22 few animals available for testing. Even with the relatively large sample size for studies of this  
23 nature (N=43, representing approximately 1/3 of the species), our analysis lacked sufficient  
24 power to confirm that birds responded statistically similarly to live predator and control  
25 treatments. However, we remain confident in our general findings because numerical trends

1 suggested similar increases in anti-predator behaviour across treatments. By adding multiple  
2 controls to our setup, we increased the effort and sample size needed, but were able to better  
3 assess the efficacy of our training. Had we just included the live chicken control, we would  
4 have been unable to determine if ‘alalā generalized their responses to animate avian stimuli, or  
5 if they sensitized to the setup, and either conclusion could lead to different survival outcomes.  
6 Specifically, if birds were merely sensitized to the training, they would not likely respond with  
7 anti-predator behaviour to actual predators post-release, because the diverse contexts where  
8 they encounter predators would not mirror the exact training setup.

9       Even if conducting two types of controls is not possible, there are other benefits to  
10 approaching training with learning in mind. For example, anti-predator training relies on  
11 tapping into social cues and reliable predator-relevant cues (Griffin, 2004; Shier & Owings,  
12 2007), but the social environment and types of cues used can both influence learning outcomes.  
13 The social environment contributed to the expression of anti-predator behaviour we  
14 documented, with larger groups of birds demonstrating more anti-predator behaviour in all  
15 trials. However, our findings do not indicate that group size influenced learning. Whether the  
16 training was more effective in larger ‘alalā groups requires further evaluation, but in other  
17 species matching natural social groupings improves training outcomes (Shier & Owings,  
18 2007). Additionally, alarm calls are potent cues for corvids (Coomes et al., 2019), and the calls  
19 we played during fear conditioning trials proved highly effective in producing fear, even  
20 without predators present. For instance, the chicken was intended to be a non-threatening,  
21 animate stimulus, but was unexpectedly fear-inducing for ‘alalā. Other birds have learned to  
22 fear novel and otherwise non-threatening animals and inanimate objects when paired with  
23 alarm calls (Curio, 1978), which may have occurred in our trials.

24       Documenting learning requires a baseline measure of behaviour, which can also help  
25 assess training needs. ‘Alalā showed high levels of anti-predator behaviour towards the model

1 predator during baseline assessments, corroborating and strengthening similar evidence from a  
2 separate study on a smaller set of juvenile released ‘alalā (Greggor et al., 2021). Together, these  
3 results suggest that much of the species is not naïve to ‘io as a threat, despite their generations  
4 in human care. It is unclear whether their baseline predatory wariness stems from observing  
5 the few resident ‘io near the facility, or has been maintained through multiple generations in  
6 conservation breeding (contrary to other species’ declines in anti-predator behaviour, e.g.,  
7 (Kraaijeveld-Smit et al., 2006). Although vulnerability to predators may have contributed to  
8 losses seen in historical (U.S. Fish and Wildlife Service, 2009) and recent translocations  
9 (Greggor et al., 2021), ‘alalā’s high baseline anti-predator responses suggest that ‘alalā  
10 recognize ‘io as a threat. Other aspects of predatory evasion—such failing to act appropriately  
11 after recognizing a predator, vigilance levels in the absence of a detected predator, or using  
12 habitat in ways that minimize vulnerability—may present greater issues (Greggor et al., 2021).  
13 Systematically addressing these components of predation risk and other threats post-release  
14 contributes to an adaptive management approach, while also improving the theory and  
15 application of translocation biology (Seddon et al., 2007; Taylor et al., 2017). An additional  
16 advantage of documenting baseline behaviour in anti-predator training is that it can be a  
17 screening tool to evaluate individual competency, can be compared with target behaviours of  
18 wild individuals, and allows for assessing inter-individual variation.

19 Ideally released animals respond fearfully to predators and only to predators. We have  
20 shown the difficulty, yet necessity of approaching anti-predator training from a cognitive  
21 standpoint to document this type of predator-specific learning. Concurrently, however, more  
22 work is needed to determine if other processes, such as sensitization or generalization, can still  
23 provide benefits, post-release. Even simple sensitization could make less-reactive animals  
24 more wary and vigilant if triggered close to release, which could be beneficial, depending on  
25 the prevalence of predators. However, generalized fear responses could levy serious costs if

1 they divert attention from other fitness-enhancing activities (Carthey & Banks, 2014). Training  
2 controls that allow managers to identify vulnerabilities to over-responding may explain  
3 unplanned losses of animals and allow release programs greater effectiveness in adaptively  
4 managing training and post-release conditions in future. Focusing on an evidence-based  
5 approach to translocation biology offers promise for improving outcomes and prioritizing  
6 interventions with higher probabilities of success, including for behavioural-based  
7 interventions such as pre-release training (Berger-Tal et al., 2020; Seddon et al., 2007).  
8 Therefore, testing the efficacy of actions involved in translocations, especially those are labour  
9 intensive, such as anti-predator training, will help support greater conservation progress  
10 overall.

#### 11 **Data Statement**

12 All data and code used for the analysis in this paper is contained within the supplementary  
13 material.

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