

Memory retention of conditioned aversion training in New Zealand's alpine parrot, the kea

Lydia R. W. McLean¹  | Margaret M. Nichols² | Alex H. Taylor³ | Ximena J. Nelson¹

¹School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

²Zero Invasive Predators Ltd, PO Box 9267 Marion Square, Wellington 6141, New Zealand

³School of Psychology, University of Auckland, 23 Symonds Street, Auckland 1010, New Zealand

Correspondence

Lydia McLean, Private Bag 4800, Christchurch 8140, New Zealand.
Email: lydiamclean@gmail.com

Funding information

University of Canterbury,
Grant/Award Number: Doctoral Scholarship;
Templeton World Charity Foundation,
Grant/Award Number: TWCF0310

Abstract

New Zealand pest control operations commonly deploy toxic sodium fluoroacetate (1080) baits to control introduced mammalian predators and protect vulnerable native fauna, yet the highly intelligent kea (*Nestor notabilis*) is at risk of mortality following ingestion of toxic baits intended for their protection. We tested the retention of conditioned aversion in 11 captive kea that had learned to avoid baits containing the bird repellent anthraquinone alongside color, olfactory, and taste cues. We revisited kea over increasing time intervals (3 days, 5 weeks, 3 months, 6 months, and 1 yr) offering them otherwise identical non-repellent baits. Kea retained their aversion until the final session, 1 year after previous exposure to reinforcement, and almost 2 years since previous exposure to repellent. Whether the kea forgot their aversion or the repeated exposures to non-repellent baits resulted in extinction of the aversion, our results indicate that kea are capable of remembering an aversion for long enough to be of practical use to conservation managers in reducing kea mortality through 1080 operations.

KEYWORDS

conditioned aversion, conservation behavior, conservation management, kea, learning, *Nestor notabilis*, parrot

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

Aversion as a result of associative conditioning is a common adaptive trait that reduces an individual's risk of exposure to potentially toxic foods by associating sensory cues with nausea (Garcia et al. 1974). To produce a long-lasting aversion, novel stimuli must be reinforced by consequences (Hadamitzky et al. 2015) such as emesis, which is energetically costly because it affects an animal's ability to consume any food for a period of time (Meehan and Riccio 2008). It is therefore advantageous for aversions to be quickly learned from a highly salient stimulus to produce a long-lasting aversion that is sufficient to result in future avoidance.

More generally, conditioned aversion responses can be deliberately induced to prevent human-wildlife conflict or for conservation management practices. For example, coyotes (*Canis latrans*) can be deterred from eating livestock and poultry (Ellins and Catalano 1980), food crops can be protected from scavengers (Pebsworth and Radhakrishna 2020), or animals can be trained to respond to novel predators (Griffin et al. 2000). Furthermore, by manipulating the outcome of an encounter with a toxic food source, it is possible for conservation managers to effectively mediate a conditioned taste response in wild animals. This has been trialed in several native Australian species that are at risk of ingesting the toxic introduced cane toad (*Rhinella marina*), including northern quolls (*Dasyurus hallucatus*; O'Donnell et al. 2010), goannas (*Varanus panoptes*; Ward-Fear et al. 2016, 2017), and blue-tongue lizards (*Tiliqua scincoides*; Price-Rees et al. 2011). Conservation managers have also deliberately induced conditioned taste aversion to reduce depredation by introduced foxes (*Vulpes vulpes*) on native species (e.g., eggs of hooded plovers [*Thinornis rubricollis*]; Maguire et al. 2010, or red-legged partridges [*Alectoris rufa*]; Tobajas et al. 2020).

The kea (*Nestor notabilis*) is an endangered alpine parrot species (BirdLife International 2017), endemic to the mountains of the South Island of Aotearoa New Zealand. Known to be highly intelligent (Gajdon et al. 2006, O'Hara et al. 2016, Goodman et al. 2018, Bastos and Taylor 2020, Laschober et al. 2021), kea are adapted to a changeable environment, and primarily forage on the ground for a wide variety of foods, including berries, leaves, roots (Brejaart 1988, Young et al. 2012, Greer et al. 2015), invertebrates (O'Donnell and Dilks 1994, Greer et al. 2015), and scavenged meat (Schwing 2010). Kea will readily investigate novel objects for edibility (Reid 2008), and, unusually for birds, they retain neophilia (Diamond and Bond 1991) and play behaviors (Diamond and Bond 2003) into adulthood, which may be a product of the need for lifelong learning in an unpredictable environment. Indeed, adult kea have sometimes proven more explorative in the wild than younger conspecifics (Gajdon et al. 2006, Goodman et al. 2018). Harmful anthropogenic substances therefore pose a risk to kea of all ages, and documented cases of illness or mortality have been linked to ingestion of lead (McLelland et al. 2010, Reid et al. 2012), chocolate (Gartrell and Reid 2007), and fiberglass insulation (Temple 1994), among others.

Throughout their habitat, kea are regularly exposed to sodium fluoroacetate (1080; New Zealand Department of Conservation 2020). This poison is deployed in cereal bait pellets from helicopters to target mammalian predators, such as rats (black rat [*Rattus rattus*]; Polynesian rat [*R. exulans*], Norway rat [*R. norvegicus*]) and brushtail possums (*Trichosurus vulpecula*) and, by way of secondary poisoning from consuming rodent carcasses, stoats (*Mustela erminea*; Murphy et al. 1999, Elliott and Kemp 2016). Currently, aerially deployed 1080 is the most effective means to protect endangered native species, by removing invasive predators from New Zealand's terrestrial ecosystems on a landscape scale (Elliott and Kemp 2016). While kea, which are famously charismatic birds (Schwing et al. 2017), are at high risk of directly consuming toxic baits (Orr-Walker and Roberts 2009, Kemp et al. 2019, New Zealand Department of Conservation 2020), 1080 operations provide an overall benefit to kea populations by enabling increased nesting success in subsequent breeding seasons. Monitored kea nests within a 1080 control zone were almost 7 times more likely to survive to fledging than those outside of the control zone (Kemp et al. 2018). The use of 1080 in New Zealand is controversial, and recorded deaths of kea are widely reported to the public. To maintain social license to use 1080 and to maximize the benefits of 1080 operations to this endangered species, efforts should be made to reduce by-kill.

Strategies to prevent by-kill include incorporation of primary bird repellents, such as green dye (Hartley et al. 1999, 2000; Weser and Ross 2013) and cinnamon lure (Hickling 1997, Cowan and Crowell 2017), and regulations permitting only the use of the less-preferred RS5 bait matrix in kea habitat (Blyth 2011, New Zealand Department

of Conservation 2020). Anthraquinone is a taste-based bird repellent (Poché 1998) commonly used for crop protection (Werner et al. 2011, 2015), which holds potential as an additional tool to prevent non-target interactions with toxic baits. In contrast to primary repellents, anthraquinone is a secondary repellent that produces gastrointestinal discomfort (Avery et al. 1997), meaning a bird has to consume and suffer ill-effects of the repellent to learn an aversion. Anthraquinone is an effective repellent in black rats and brushtail possums (Cowan et al. 2015). This poses logistical challenges for conservation managers trying to administer repellent in such a way that it is not accessible to target species of 1080 operations. Baits containing anthraquinone have proved a successful deterrent for New Zealand North Island robins (*Petroica australis longipes*) and tomtits (*P. macrocephala toitoi*; Clapperton et al. 2014) from consuming cereal baits, while captive trials have demonstrated a reduction in consumption of baits by kea (Orr-Walker et al. 2012, Reardon 2014). Nichols et al. (2020) undertook a recent trial on captive kea to determine whether consumption of baits containing anthraquinone (alongside visual and olfactory cues) could lead to an aversion strong enough to avoid a hypothetical lethal dose of 1080. This study proved anthraquinone to be a potent repellent for kea, resulting in all subjects entirely ceasing to interact with baits following conditioning.

The suitability of anthraquinone as a tool for use on wild kea hinges on whether they will retain an aversion for long enough to avoid baits through a 1080 operation, which, depending on the timing of the aversion training, could be several months. With the aim of determining the duration of kea aversion to cereal baits, we tested the memory of bait aversion, with ever-increasing time intervals, in the same group of captive kea as Nichols et al. (2020), beginning shortly after the aversion was developed.

STUDY AREA

Trials took place on 11 captive adult kea (8 male, 3 female, all individually marked with colored leg bands) housed together in a walk-through enclosure measuring approximately 40 m × 25 m (~1,000 m²) at Willowbank Wildlife Reserve in Christchurch, New Zealand. The large outdoor aviary mimics the kea's natural environment, with native trees and bushes, varying topography, 2 secluded nesting shelters, a stream, and a large pond, enabling kea to exhibit natural feeding, grooming and social behavior. The reserve is on the edge of the city at sea level, approximately 100 km from the nearest wild kea population, and weather and climate conditions are within the

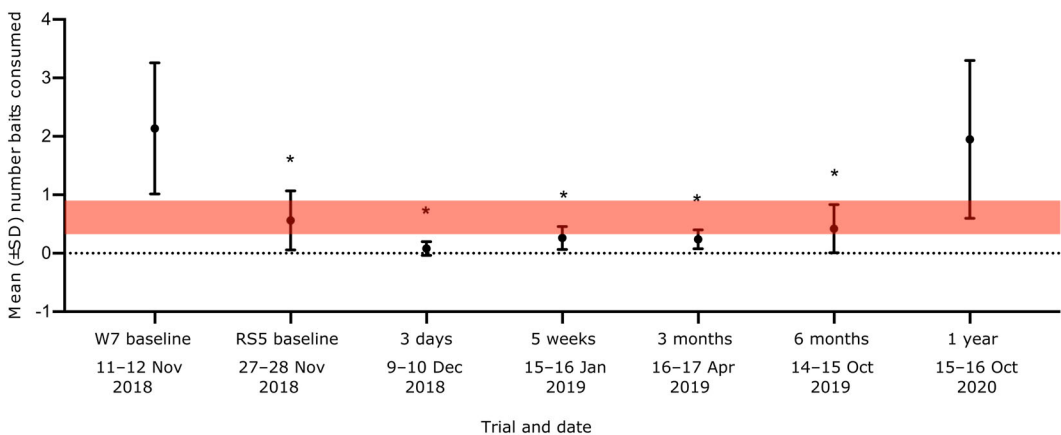


FIGURE 1 Mean (±SD) number of baits consumed by captive kea at each time interval in a memory retention trial at Willowbank Wildlife Reserve, Christchurch, New Zealand, 2018–2020. Asterisks (*) indicate a significant difference ($P < 0.05$) from Wanganui 7 (W7) baseline. Shaded rectangle represents upper and lower median lethal dose (LD50) estimates, based on parrot species of a similar size (Orr-Walker et al. 2012).

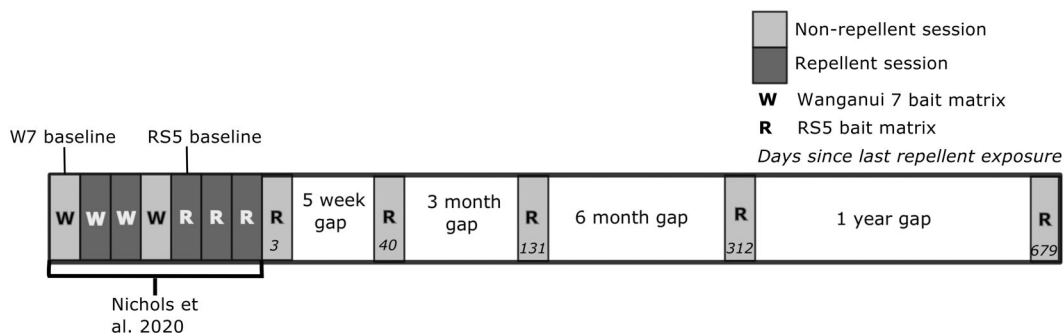
kea's natural range. The kea are accustomed to hundreds of visitors passing through the enclosure each day and most will readily interact with people, yet they are able to retreat to areas out of sight of visitors. The kea are fed daily from 3 self-operated feeding stations mounted on poles to prevent access to rodents. We withheld food from kea until after trials were completed each day, at about 1000. The kea receive daily enrichment activities and regularly take part in behavior and cognition studies (Bastos and Taylor 2020). Trials took place from November 2018 until October 2020, with sessions in spring (Oct–Nov), summer (Dec–Jan) and fall (Apr; Figure 1).

METHODS

Our study was a follow-up to an aversion learning trial by Nichols et al. (2020). We conducted all sessions in an identical manner to those described by Nichols et al. (2020) to ensure the kea were exposed to the same stimuli as they had encountered when learning the conditioned aversion. Kea welfare was our highest priority, and the enclosure and conditions in which they are housed exceeded the requirements of the New Zealand Department of Conservation's captive management plan (Pullar 1996). We did not force kea to participate in the study and they could retreat to an inaccessible area of the enclosure (e.g., treetops, nesting houses) at any time. Each session took place over 2 consecutive mornings, starting at 0800 and ending when all kea refused to consume or interact with baits. A team of 3–5 observers handed baits directly to kea. The observers were distributed throughout the enclosure to ensure every kea had the opportunity to consume baits. In many cases observers actively pursued kea so that less-dominant individuals could also be tested. Observers estimated consumption to the nearest quarter of a bait. If a kea finished a bait, or dropped it in an inaccessible place, the observer would continue to administer more baits until the kea ceased to participate in the session. In some cases, a bait would be stolen by another kea so observers would estimate the proportion consumed by each. Observers wore full face masks throughout every session to ensure that kea were taking cues from the appearance of the baits rather than from individual people.

All baits were manufactured by Orillion Ltd (Whanganui, New Zealand) using 2 cereal matrices identical to those deployed in aerial poison operations in New Zealand: Wanganui 7 (W7) are harder (Bowen et al. 1995) and scented with orange, while RS5 break down more readily and are scented with cinnamon. All baits were dyed green, cylindrical in shape, and weighed approximately 6 g.

Baseline consumption of W7 bait was recorded by Nichols et al. (2020) prior to any aversion training. During subsequent sessions, Nichols et al. (2020) exposed the kea to W7 baits containing 2.7% anthraquinone, a repellent



that produces gastrointestinal discomfort and nausea in birds (Poché 1998). After 3 sessions of exposure to repellent W7 baits, all 11 kea had learned an aversion and consumption dropped to zero for all birds. They then tested the RS5 matrix (i.e., RS5 baseline) because our study only used RS5 baits for all follow-up sessions. We include both the W7 and the RS5 baselines in our analyses.

We then revisited the kea over increasing time intervals to test their memory of the aversion, using non-repellent RS5 baits at every visit. The follow-up sessions took place with roughly a doubling of the time of the previous intervening period after the first trial, which occurred 3 days after the final repellent exposure. After this, memory retention trials took place after 5 weeks, then doubled to 3 months after that, then to 6 months, and 1 year, such that the total experimental duration was almost 2 years (Figures 1 and 2).

We quantified memory of the aversion by measuring the amount of bait eaten by each bird during each session to the nearest quarter. We averaged each kea's consumption over the 2 days of each session to reduce the influence of weather and keeper activities. To compare consumption at each time interval, we conducted a repeated-measures analysis of variance with a Geisser-Greenhouse correction, comparing bait consumption at each session to both the original W7 baseline and the RS5 baseline. We used Bonferroni corrections for multiple comparisons to determine whether overall bait consumption during each session was significantly different to that of the W7 and RS5 baselines.

RESULTS

Bait consumption (Table 1; Figure 1) differed significantly between sessions ($F_{6,10} = 19.51$, $P < 0.001$). *Post hoc* tests revealed that relative to the W7 baseline, kea ate less RS5 bait on their first exposure to the new bait type ($\bar{x} = 1.6$ fewer baits; $P = 0.02$); we determined W7 baseline prior to aversion training and the first exposure to RS5 took place after aversion training to W7 baits. Consumption in all subsequent sessions was reduced ($P < 0.05$ for all comparisons) except for the final session after a 1-year gap, during which consumption increased to a level not different to the W7 baseline ($P = 0.99$). Relative to the RS5 baseline, bait consumption did not differ in any subsequent session except for the final 1-year follow-up, during which consumption was higher than the RS5 baseline ($\bar{x} = 1.4$ more baits consumed, $P = 0.05$).

DISCUSSION

Following the conclusion of Nichols et al. (2020) that kea can learn an aversion to cereal pellets containing 2.7% anthraquinone, we have demonstrated that this aversion will persist for over 10 months (320 days) since the last exposure to baits containing repellent (from 28 Dec 2018 to 14 Oct 2019), even after exposure to non-repellent

TABLE 1 Descriptive statistics of bait consumption (number of baits) by 11 captive kea throughout all memory retention sessions that took place at Willowbank Wildlife Reserve, Christchurch, New Zealand, 2018–2020.

Descriptor	Wanganui 7 baseline	RS5 baseline	3 days	5 weeks	3 months	6 months	1 year
Min.	0.0	0.0	0.0	0.0	0.0	0.0	0.0
25th percentile	1.6	0.2	0.0	0.1	0.1	0.0	0.2
Median	2.0	0.4	0.0	0.3	0.3	0.4	2.5
75th percentile	3.0	1.0	0.2	0.4	0.3	0.8	2.8
Max.	4.1	1.6	0.3	0.6	0.6	1.3	3.8

baits on 4 occasions in the interim. Whether we used W7 or RS5 as the baseline did not change this result: in both cases the only significant change in feeding rate, after initial exposure to each bait type, occurred at the 12-month mark, so it was only after 1 year with no intervening reinforcement that consumption of baits increased to a level comparable to the first session. In the intervening period, bait consumption dropped from above the estimated upper median lethal dose (LD50) limit of 0.8 baits to roughly below the lower LD50 estimates (0.3 baits) that have been calculated based on Australian parrots of a similar size (Orr-Walker et al. 2012).

There are 2 feasible reasons why consumption increased in the final session. First the kea may have forgotten their learned aversion to baits. Alternatively, the aversion response may have been attenuated by repeated exposures to non-repellent baits, leading to an extinction of the aversion. Extinction occurs when the conditioned response is reduced following repeated exposures to the conditioned stimulus alone following conditioning (Pavlov 1927). In this case, the kea were exposed to non-repellent baits during 4 sessions (8 days) before they resumed consumption close to baseline levels on the fifth re-exposure. During these sessions, kea bait consumption was low but was nevertheless greater than zero. A few cautionary nibbles in preceding sessions may have been sufficient for the aversion to become extinct.

Our study aimed to simulate the circumstances that may occur in an *in situ* poison operation in kea habitat. The 1080 operations are generally preceded by distribution of non-toxic pre-feed baits that are very similar in appearance to the toxic baits that follow, albeit without the green dye in most cases. Pre-feed is aurally distributed ahead of toxic baits to aid target species (especially rats) to overcome the innate neophobia towards new foods to ensure a lethal dose of toxic bait is later consumed (Ross et al. 2000, Nugent et al. 2019). In some circumstances, pre-feed is dropped twice before distribution of toxic baits (Nugent et al. 2019). If wild kea were aversion-trained with anthraquinone-laced baits prior to any pre-feed, our results suggest that the aversion would be retained throughout intervening pre-feed exposures long enough to provide protection from toxic baits, as it was only on the fifth exposure to a non-repellent bait that kea ate a sufficient amount of the bait for a potentially lethal dose.

There are a number of caveats to our findings. First, all animals tested here were adults. There is evidence of ontogenetic differences in retention of taste aversions in rats (Martinez and Rigter 1983) and chicks (Hayne et al. 1996), with younger individuals of both species more likely to overcome an aversion. Kea have a protracted juvenile period (Moorhouse and Greene 1995) and exhibit age-related differences in foraging strategy (Diamond and Bond 1991), so further studies on kea should aim to include younger individuals to determine how ontogeny affects aversion learning and retention. Secondly, only 3 female kea were included in our trial, and 1 of these did not interact with any anthraquinone-laced baits during aversion training (Nichols et al. 2020). The time of year at which Nichols et al. (2020) conducted the aversion training corresponds to nesting season in kea, which may have affected female participation in the trial. Female kea differ from males in behavior (Diamond and Bond 1999) and diet (Greer et al. 2015), which may to some extent explain the limited female participation in these captive trials. Female interactions need to be better understood to apply these findings to conservation management practices. Female kea currently exist in the wild in much lower numbers than males (Laura Young, New Zealand Department of Conservation, personal communication) and their survivorship through reproductive years is critical for the population to endure. Third, there is evidence that the context in which an aversion is learned is important for memory retention, and a change in context may result in attenuation of the aversion (Spear and Riccio 1994). This is relevant because the first exposure to RS5 baits took place after kea had already learned an aversion to W7 pellets, and both bait types were delivered in the same context and had the same appearance, with the only differences being in texture and scent (Nichols et al. 2020). Consequently, to interpret our results, the W7 baseline provides a more reliable comparison by which to measure subsequent consumption than the RS5 baseline, as initial consumption of RS5 baits (Nichols et al. 2020) by kea was therefore likely lower than it would have been had they not already learned an aversion to W7 baits. Blyth (2011) reported, however, that kea preferred the W7 bait matrix to RS5, which may partly explain the lower consumption of RS5 in our study relative to the W7 baseline, but the increase in consumption of RS5 baits in the final session to levels comparable to the W7 baseline implies this preference is insufficient to prevent them from eating RS5 baits.

In relation to the context in which an aversion is learned, in a practical context, pellets containing anthraquinone must be administered to wild kea in such a way that they are not accessible to target pests, as mammals can also learn an aversion to baits containing anthraquinone and have long-lasting memory of aversion (Ogilvie et al. 2000, Clapperton et al. 2015). Thus, to condition kea, but not the 1080-target animals, anthraquinone-laced baits must be distributed in a dispenser or location (e.g., high altitude) that only kea can access. As the latter stages of 1080 poison operations scatter pre-feed and toxic baits on the ground, future work should consider whether a change in method of bait dispensing between aversion training and exposure to toxic baits affects aversion. In this captive trial, all baits were dispensed directly by a human observer, which may in itself be a cue associated with the aversion. To mimic learning conditions in the wild, further studies should distribute baits directly from a dispenser. This may, however, reduce interaction rates and introduce bias from social hierarchies that enable certain individuals to control access to resources. Whether kea are capable of accessing sufficient baits to learn an aversion from a dispenser in a wild context remains to be tested. Furthermore, because of the multi-year gap between 1080 operations in an area, reinforcement training would be necessary in subsequent operations to prompt the aversion and to reach newly recruited individuals in the operation zone.

Despite these caveats, our study provides evidence that, remarkably, kea can retain a learned aversion for close to a year. Shaw and Harvey (2020) reported similar results for New Zealand robins. In a practical sense, this offers conservation managers a wide window for beginning aversion training well ahead of a planned 1080 operation.

MANAGEMENT IMPLICATIONS

The 1080 operations in kea habitat can result in accidental by-kill of this endangered species. Our study provides evidence that kea can learn an aversion to pellets resembling those used in 1080 operations for close to a year with no attenuating reinforcement. This provides conservation managers with an opportunity to undertake aversion training in wild kea populations ahead of a planned poison operation. Our study contributes towards the development of a workable solution to aversion training in the wild, and this promising result deems further development of aversion training methodology worthwhile.

ACKNOWLEDGMENTS

We thank the volunteers for this study: A. P. M. Bastos, R. Johnston, G. Venable, M. M. Bird, M. J. Eatson, J. J. Wardle, A. L. Moser-Rust, B. Humphrey. We are grateful to N. Ackroyd and the team at Willowbank for access to the kea enclosure and support of our study. Zero Invasive Predators supplied baits to ensure the continuity of this study with previous aversion trials. L. M. was funded by a University of Canterbury Doctoral Scholarship and X. J. N. and A. H. T. received a Templeton World Charity Foundation grant (TWCF0310). Open access publishing facilitated by University of Canterbury, as part of the Wiley-University of Canterbury agreement via the Council of Australian University Librarians.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support this research will be openly available in Dryad.

ETHICS STATEMENT

This project was undertaken with approval from Lincoln University Animal Ethics Committee (AEC 2018-44).

ORCID

Lydia R. W. McLean  <https://orcid.org/0000-0001-9413-9967>

REFERENCES

- Avery, M. L., J. S. Humphrey, and D. G. Decker. 1997. Feeding deterrence of anthraquinone, anthracene, and anthrone to rice-eating birds. *Journal of Wildlife Management* 61:1359–1365.
- Bastos, A. P., and A. H. Taylor. 2020. Kea show three signatures of domain-general statistical inference. *Nature Communications* 11:828.
- BirdLife International. 2017. *Nestor notabilis*. The IUCN Red List of Threatened Species 2017:e.T22684831A119243358. <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22684831A119243358.en>. Accessed 8 Oct 2021.
- Blyth, R. 2011. Comparative bait preference in captive kea (*Nestor notabilis*). RMB Consultants Ltd. Report for the Animal Health Board, Wellington, New Zealand.
- Bowen, L., D. Morgan, and C. Eason. 1995. Persistence of sodium monofluoroacetate (1080) in baits under simulated rainfall. *New Zealand Journal of Agricultural Research* 38:29–531.
- Brejaart, R. 1988. Diet and feeding behaviour of the kea (*Nestor notabilis*). Dissertation, Lincoln University, Canterbury, New Zealand.
- Clapperton, B. K., T. D. Day, D. K. J. Morgan, F. Huddart, N. Cox, and L. R. Matthews. 2015. Palatability and efficacy to possums and rats of pest control baits containing bird repellents. *New Zealand Journal of Zoology* 42:104–118.
- Clapperton, B. K., D. K. J. Morgan, T. D. Day, K. E. Oates, A. M. Beath, N. R. Cox, and L. R. Matthews. 2014. Efficacy of bird repellents at deterring North Island robins (*Petroica australis longipes*) and tomtits (*P. macrocephala toitoi*) from baits. *New Zealand Journal of Ecology* 38:116–123.
- Cowan, P., S. Brown, G. Forrester, L. Booth, and M. Crowell. 2015. Bird-repellent effects on bait efficacy for control of invasive mammal pests. *Pest Management Science* 71:1075–1081.
- Cowan, P., and M. Crowell. 2017. Visual and taste cues for minimising native bird interactions with toxic 1080 baits—a review of current practices. *New Zealand Journal of Ecology* 41:178–185.
- Diamond, J., and A. B. Bond 1991. Social behavior and the ontogeny of foraging in the kea (*Nestor notabilis*). *Ethology* 88: 128–144.
- Diamond, J., and A. B. Bond. 1999. Kea, bird of paradox: the evolution and behavior of a New Zealand parrot. University of California Press, Berkeley, USA.
- Diamond, J., and A. B. Bond. 2003. A comparative analysis of social play in birds. *Behaviour* 140:1091–1115.
- Ellins, S. R., and S. M. Catalano. 1980. Field application of the conditioned taste aversion paradigm to the control of coyote predation on sheep and turkeys. *Behavioral and Neural Biology* 29:532–536.
- Elliott, G., and J. Kemp. 2016. Large-scale pest control in New Zealand beech forests. *Ecological Management & Restoration* 17:200–209.
- Gajdon, G. K., N. Fijn, and L. Huber. 2006. Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Animal Cognition* 9:173–181.
- García, J., W. G. Hankins, and K. W. Rusiniak. 1974. Behavioral regulation of the milieu interne in man and rat. *Science* 185: 824–831.
- Gartrell, B. D., and C. Reid. 2007. Death by chocolate: a fatal problem for an inquisitive wild parrot. *New Zealand Veterinary Journal* 55:149–151.
- Goodman, M., T. Hayward, and G. R. Hunt. 2018. Habitual tool use innovated by free-living New Zealand kea. *Scientific Reports* 8:13935.
- Greer, A. L., G. K. Gajdon, and X. J. Nelson. 2015. Intraspecific variation in the foraging ecology of kea, the world's only mountain-and rainforest-dwelling parrot. *New Zealand Journal of Ecology* 39:254–261.
- Griffin, A. S., D. T. Blumstein, and C. S. Evans. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology* 14:1317–1326.
- Hadamitzky, M., K. Bösche, A. Engler, M. Schedlowski, and H. Engler 2015. Extinction of conditioned taste aversion is related to the aversion strength and associated with c-fos expression in the insular cortex. *Neuroscience* 303:34–41.
- Hartley, L., C. O'Connor, J. R. Waas, and L. R. Matthews. 1999. Colour preferences in North Island robins (*Petroica australis*): implications for deterring birds from poisonous baits. *New Zealand Journal of Ecology* 23:255–259.
- Hartley, L., J. R. Waas, C. O'Connor, and L. R. Matthews. 2000. Colour preferences and coloured bait consumption by weka *Gallirallus australis*, an endemic New Zealand rail. *Biological Conservation* 93:255–263.
- Hayne, H., C. Rovee-Collier, G. Collier, L. Tudor, and C. A. Morgan. 1996. Learning and retention of conditioned aversions by freely feeding chicks. *Developmental Psychobiology* 29:417–431.
- Hickling, G. J. 1997. Effect of green dye and cinnamon oil on consumption of cereal pest baits by captive North Island kaka (*Nestor meridionalis*). *New Zealand Journal of Zoology* 24:239–242.
- Kemp, J., C. C. Mosen, G. Elliot, and C. M. Hunter. 2018. Effects of the aerial application of 1080 to control pest mammals on kea reproductive success. *New Zealand Journal of Ecology* 42:158–168.
- Kemp, J., C. C. Mosen, G. Elliot, C. M. Hunter, and P. van Klink. 2019. Kea survival during aerial poisoning for rat and possum control. *New Zealand Journal of Ecology* 43:3351.

- Laschober, M., R. Mundry, L. Huber, and R. Schwing. 2021. Kea (*Nestor notabilis*) show flexibility and individuality in within-session reversal learning tasks. *Animal Cognition* 24:1339–1351.
- Maguire, G. S., D. Stojanovic, and M. A. Weston. 2010. Conditioned taste aversion reduces fox depredation on model eggs on beaches. *Wildlife Research* 36:702–708.
- Martinez, J. L., Jr., and H. Rigter. 1983. Assessment of retention capacities in old rats. *Behavioral and Neural Biology* 39: 181–191.
- McLelland, J. M., C. Reid, K. McInnes, W. D. Roe, and B. D. Gartrell. 2010. Evidence of lead exposure in a free-ranging population of kea (*Nestor notabilis*). *Journal of Wildlife Diseases* 46:532–540.
- Meehan, S. M., and D. C. Riccio. 2008. Memory phenomena and conditioned taste aversion. Pages 114–133 in S. Reilly and R. T. Schachtman, editors. *Conditioned taste aversion: behavioral and neural processes*. Oxford University Press, New York, New York, USA.
- Moorhouse, R. J., and T. C. Greene. 1995. Identification of fledgling and juvenile kaka (*Nestor meridionalis*). *Notornis* 42: 187–202.
- Murphy, E., L. Robbins, J. Young, and J. Dowding. 1999. Secondary poisoning of stoats after an aerial 1080 poison operation in Pureora Forest, New Zealand. *New Zealand Journal of Ecology* 23:175–182.
- New Zealand Department of Conservation. 2020. Aerial 1080 in kea habitat Code of Practice. Department of Conservation, Wellington, New Zealand.
- Nichols, M., P. Bell, N. Mulgan, and A. Taylor. 2020. Conditioned aversion in kea to cereal bait: a captive study using anthraquinone. *Applied Animal Behaviour Science* 230:105077.
- Nugent, G., G. A. Morriss, and B. Warburton. 2019. Attempting local elimination of possums (and rats) using dual aerial 1080 baiting. *New Zealand Journal of Ecology* 43:3373.
- O'Donnell, C. F., and P. J. Dilks. 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. *New Zealand Journal of Ecology* 18:87–107.
- O'Donnell, S., J. K. Webb, and R. Shine. 2010. Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology* 47:558–565.
- O'Hara, M., R. Schwing, I. Federspiel, G. K. Gajdon, and L. Huber. 2016. Reasoning by exclusion in the kea (*Nestor notabilis*). *Animal Cognition* 19:965–975.
- Ogilvie, S. C., M. D. Thomas, G. A. Morriss, D. R. Morgan, and C. T. Eason. 2000. Investigation of sodium monofluoroacetate (1080) bait shyness in wild brushtail possum (*Trichosurus vulpecula*) populations. *International Journal of Pest Management* 46:77–80.
- Orr-Walker, T., N. J. Adams, L. G. Roberts, J. R. Kemp, and E. B. Spurr. 2012. Effectiveness of the bird repellents anthraquinone and d-pulegone on an endemic New Zealand parrot, the kea (*Nestor notabilis*). *Applied Animal Behaviour Science* 137:80–85.
- Orr-Walker, T., and L. G. Roberts. 2009. Population estimations of wild kea (*Nestor notabilis*). Kea Conservation Trust, Queenstown, New Zealand.
- Pavlov, I. P. 1927. *Conditioned reflexes: an investigation of the physiological activity of the cerebral cortex* (Volume 142). Oxford University Press, London, United Kingdom.
- Pebsworth, P., and S. Radhakrishna. 2020. Using conditioned taste aversion to reduce human-nonhuman primate conflict: a comparison of four potentially illness-inducing drugs. *Applied Animal Behaviour Science* 225:104948.
- Poché, R. M. 1998. Development of a new bird repellent, Flight Control. *Proceedings of the Vertebrate Pest Conference* 18: 338–344.
- Price-Rees, S. J., J. K. Webb, and R. Shine. 2011. School for skinks: can conditioned taste aversion enable bluetongue lizards (*Tiliqua scincoides*) to avoid toxic cane toads (*Rhinella marina*) as prey? *Ethology* 117:749–757.
- Pullar, T. 1996. Kea (*Nestor notabilis*) captive management plan and husbandry manual. Threatened Species Occasional Publication Number 9. Department of Conservation, Wellington, New Zealand.
- Reardon, J. 2014. Kea repellent development report July 2014. Department of Conservation, Wellington, New Zealand.
- Reid, C. 2008. Exploration—avoidance and an anthropogenic toxin (lead pb) in a wild parrot (kea: *Nestor notabilis*). Thesis, Victoria University of Wellington, Wellington, New Zealand.
- Reid, C., K. McInnes, J. M. McLelland, and B. D. Gartrell. 2012. Anthropogenic lead (pb) exposure in populations of a wild parrot (kea *Nestor notabilis*). *New Zealand Journal of Ecology* 36:56–63.
- Ross, J., G. Hickling, D. Morgan, and C. Eason. 2000. The role of non-toxic prefeed and postfeed in the development and maintenance of 1080 bait shyness in captive brushtail possums. *Wildlife Research* 27:69–74.
- Schwing, R. 2010. Scavenging behaviour of kea (*Nestor notabilis*). *Notornis* 57:98–99.
- Schwing, R., X. J. Nelson, A. Wein, and S. Parsons. 2017. Positive emotional contagion in a New Zealand parrot. *Current Biology* 27:R213–R214.
- Shaw, R. C., and A. Harvey. 2020. Long-term memory for a learned behaviour in a wild bird. *Biology Letters* 16:20190912.
- Spear, N. E., and D. C. Riccio. 1994. *Memory: phenomena and principles*. Allyn & Bacon, Boston, Massachusetts, USA.

- Temple, P. 1994. Kea: the feisty parrot. *New Zealand Geographic* Oct–Dec 1994.
- Tobajas, J., E. Descalzo, R. Mateo, and P. Ferreras. 2020. Reducing nest predation of ground-nesting birds through conditioned food aversion. *Biological Conservation* 242:108405.
- Ward-Fear, G., D. Pearson, G. Brown, B. Rangers, and R. Shine. 2016. Ecological immunization: In situ training of free-ranging predatory lizards reduces their vulnerability to invasive toxic prey. *Biology Letters* 12:20150863.
- Ward-Fear, G., J. Thomas, J. K. Webb, D. J. Pearson, and R. Shine. 2017. Eliciting conditioned taste aversion in lizards: live toxic prey are more effective than scent and taste cues alone. *Integrative Zoology* 12:112–120.
- Werner, S. J., S. T. DeLiberto, A. M. Mangan, S. E. Pettit, J. W. Ellis, and J. C. Carlson. 2015. Anthraquinone-based repellent for horned larks, great-tailed grackles, American crows and the protection of California's specialty crops. *Crop Protection* 72:158–162.
- Werner, S. J., G. M. Linz, J. C. Carlson, S. E. Pettit, S. K. Tupper, and M. M. Santer. 2011. Anthraquinone-based bird repellent for sunflower crops. *Applied Animal Behaviour Science* 129:162–169.
- Weser, C., and J. G. Ross. 2013. The effect of colour on bait consumption of kea (*Nestor notabilis*): implications for deterring birds from toxic baits. *New Zealand Journal of Zoology* 40:137–144.
- Young, L. M., D. Kelly, and X. J. Nelson. 2012. Alpine flora may depend on declining frugivorous parrot for seed dispersal. *Biological Conservation* 147:133–142.

Associate Editor: Bill Block.

How to cite this article: McLean, L. R. W., M. M. Nichols, A. H. Taylor, and X. J. Nelson. 2022. Memory retention of conditioned aversion training in New Zealand's alpine parrot, the kea. *Journal of Wildlife Management* e22221. <https://doi.org/10.1002/jwmg.22221>