ORIGINAL PAPER

Lichen moths do not benefit from 'element imitation' masquerade in the absence of a matching background

C. J. Mark[1,4] · C. J. Painting[2] · J. C. O'Hanlon[3] · G. I. Holwell[1]

Abstract

Predation places significant selection pressures on prey species and many have evolved incredible and diverse colour patterns in response. A fascinating example of such adaptive colouration and morphology is masquerade, a camouflage strategy in which organisms resemble innocuous and inedible objects, such as leaves or twigs. Masquerading prey avoid predation by being misclassified as irrelevant parts of the environment, rather than as food. Here we assess a putative case of masquerade in the North Island lichen moth, *Declana atronivea* (Geometridae), an endemic New Zealand species with intricate black and white forewings that appear to resemble lichen. Lichen masquerade is a type of 'element imitation' in which the object being mimicked forms a common element of the environmental pattern. However, unlike discrete objects, such as leaves and twigs, lichen may be difficult to distinguish as a distinct entity. This raises the question of whether *D. atronivea* can be said to look like 'a' lichen, or whether its body colouration appears as a component of a larger patch of lichen. In this case, does the lichen resemblance function as a form of masquerade, or is it an example of background matching? Using laboratory experiments with domestic chicks (*Gallus gallus*) as predators, we investigated whether *D. atronivea* moths avoid predation by being misclassified as lichen. We exposed naïve and experienced chicks to *D. atronivea* and compared their responses, predicting that if the moths do benefit from masquerade, chicks with previous experience of lichen would take longer to attack. Our hypothesis was not supported; there was no significant difference in predator interaction regardless of prior experience, suggesting that, in the absence of a matching background, *D. atronivea* do not benefit from masquerading as lichen. Rather, this may be a case of context-dependent misclassification, or perhaps the forewing colouration promotes concealment through crypsis.

✉ C. J. Mark
  cmar167@aucklanduni.ac.nz

1   Te Kura Mātauranga Koiora|School of Biological Sciences, Te Whare Wānanga o Tāmaki
     Makaurau|The University of Auckland, Building 110, 3A Symonds Street, Auckland 1010,
     New Zealand

2   Te Aka Mātuatua School of Science, University of Waikato, Private Bag 3105, Hamilton 3240,
     New Zealand

3   School of Science and Technology, University of New England, Armidale, NSW 2351, Australia

4   Auckland, New Zealand

Introduction

The ways in which animals use colour patterns to avoid predation are diverse and extraordinary; some animals seek to completely avoid detection from predators through crypsis (Stevens and Merilaita 2009a, b; Cuthill 2019), while others enhance their conspicuousness by advertising their unpalatability through aposematism (Mappes et al. 2005; Ruxton et al. 2018). In the middle of this continuum of defence are those animals that avoid predation by remarkable visual (and sometimes behavioural) resemblance to something that is unpalatable. This may involve an innocuous and otherwise palatable mimic that resembles a species which is harmful to potential predators, such as in Batesian mimicry, where the mimicking organism gains protection through deceiving predators into misidentifying them as the defended 'model' species (Quicke 2017; Font 2019). Other animals employ a similar yet distinct mechanism whereby they resemble uninteresting objects from their environment, such as a leaf (Kuntner et al. 2016), twig (Skelhorn et al. 2010b), lichen (Toledo and Haddad 2009), or bird droppings (Liu et al. 2014). This type of camouflage strategy is known as masquerade and acts to hinder correct recognition, so that while predators may detect the prey, they misclassify them as something of no value (Skelhorn et al. 2010a).

The general idea of masquerade has been acknowledged for over a century (e.g. Poulton 1890; Thayer 1918; Carrick 1936; Cott 1940; Edmunds 1974; Endler 1981; Robinson 1981; Allen and Cooper 1985), yet despite the assumed antipredatory function, this defensive strategy only recently received empirical attention, and definitive evidence for the adaptive value of such resemblances has only been demonstrated in the last decade (Skelhorn and Ruxton 2010, 2011a, b; Skelhorn et al. 2010b, c). This is perhaps because distinguishing between masquerade and other forms of camouflage, such as background matching, poses a methodological challenge (Skelhorn et al. 2010a). Unlike cryptic prey that are adapted to blend into the background and avoid detection, masquerading organisms are clearly distinguishable as an object. The inherent value of masquerade is in not being recognised as potential prey (Ruxton et al. 2018). Thus, to demonstrate the defensive benefit of masquerade, it must be shown that a predator has detected the prey item but failed to recognise it as a food resource. Furthermore, to be able to misidentify masquerading prey as the object that they resemble, predators must first have had experience with that model object. Skelhorn et al. (2010b) developed an experimental design to test this using twig-mimicking caterpillars (as prey) and naïve chicks (as predators). By manipulating the prior experiences of the predators to the putative masquerade model (twigs) while keeping their exposure to the masquerading prey the same, the researchers were able to demonstrate that chicks who had previously encountered the twigs were slower to attack the caterpillars than those with no experience of the twigs or who were presented with manipulated twigs (that no longer resembled caterpillars). The chicks with experience of twigs applied their learned disinterest to the twig-mimicking caterpillars, misclassifying them as a non-food component of their environment and thereby demonstrating that the caterpillars were benefiting from masquerade.

Following on from this work (Skelhorn et al. 2010b), other studies extended on these findings to elucidate some of the underlying mechanisms of this camouflage strategy (Skelhorn et al. 2010c; Skelhorn and Ruxton 2011a, b, 2013; Higginson et al. 2012). However, it is still uncertain how prevalent masquerade is in nature. Masquerade has been suggested

to occur in a wide array of taxa, including potential examples from among the stick and leaf insects (Phasmatodea), with their uncanny stick-like appearance, and the numerous stick-mimicking caterpillars of geometrid moths (de Ruiter 1951; Skelhorn et al. 2010b; Skelhorn and Ruxton 2010). Other caterpillars bear striking resemblance to bird droppings (Skelhorn 2015; Suzuki and Sakurai 2015), as do some *Phrynarachne* crab spiders (Cott 1940; Starrett 1993). Various animals also resemble fresh or dead leaves, including the ghost mantis, *Phyllocrania paradoxa* (Edmunds 1972; Skelhorn 2015), the satanic leaf-tailed gecko (*Uroplatus phantasticus*), the Malayan leaf frog (*Megophrys nasuta*) (Quicke 2017), and the Amazon fish, *Monocirrhus polycanthus* (Skelhorn et al. 2010a). Birds from the families Nyctibiidae (potoos) and Podargidae (frogmouths) have morphological and behavioural adaptations that cause them to appear remarkably like tree stumps or broken branches (Cott 1940; Skelhorn 2015; Quicke 2017). Despite the apparent pervasiveness of this camouflage strategy, the use of masquerade has mostly been inferred through human perception and very few studies have objectively and conclusively demonstrated such adaptive resemblances. It is important that we continue to quantify masquerade in more systems so that we may gain a thorough understanding of how broadly applicable this concept is in nature.

Masquerade has previously been divided into two separate phenomena based on the type of model resembled and its environmental context: 'element imitation' (or cryptic mimesis) and 'object imitation' (phaneric mimesis) (Hailman 1977; Pasteur 1982; Toledo and Haddad 2009). The former denotes a resemblance to objects that form a common or dominant element of the environment, such as leaves and twigs, whereas object imitators resemble more isolated objects that are not part of the regular environmental pattern, such as bird-droppings (Hailman 1977; Pasteur 1982; Toledo and Haddad, 2009). The important distinction between the two is that element imitators are more likely to be viewed in association with the objects they mimic and thus potentially gain additional benefits of crypsis, whilst object imitators tend to be seen in isolation of their models and may be misclassified over a wider range of backgrounds (Skelhorn et al. 2010a, b, c; Skelhorn and Ruxton 2010). In this regard, element imitators may also be under stronger selection to look more like their models (Skelhorn and Ruxton 2010).

Many of the examples above demonstrate special resemblance to discrete objects within an animal's environment, but the concept of masquerade can also be applied to animals which bear similarity to objects that are less discrete. For example, the idea of 'lichen' masquerade has been hypothesised in a number of groups, including katydids (Nickle and Castner 1995; Braun 2011), grasshoppers (Glime 2017), geckos (Cottt 1940), and frogs (Toledo and Haddad 2009; Leite et al. 2012; Glime and Boelema, 2017). Lichen masquerade can be considered a form of element imitation, yet unlike discrete objects, such as leaves and twigs, which arguably have distinguishable outlines, lichen is more variable in shape and size, and thus what constitutes the 'edges' of a piece of lichen may be harder to recognise. Furthermore, lichen often covers the surfaces of other objects in the environment, making it potentially more difficult to detect as a distinct entity. This raises the question of whether animals that resemble lichen can be said to look like 'a' lichen, or a component of a larger patch of lichen. In this case, does lichen resemblance then function as a form of masquerade, or is it an example of background matching?

The North Island lichen moth, *Declana atronivea* Walker, 1865 (Lepidoptera: Geometridae) offers an intriguing system to investigate defensive colouration. This endemic moth is distributed within pockets of native forest across the North Island of New Zealand where it is sometimes found resting on lichen-covered trees (Sharell 1971). The moth itself possesses forewings with intricate black and white patterns and discreetly textured wing scales

that to the human eye are akin to lichen (Fig. 1). This resemblance to lichen, along with the moth's apparent partiality for resting on or near lichen, has led to the suggestion that *D. atronivea* employs crypsis as a camouflage strategy; its colouration allows it to blend into the lichen through background matching. However, *D. atronivea* often alights on other substrates including moss, bark, leaf litter, and branches (pers. obs.), where they may be more obvious to predators. Camouflage theory would suggest that movement away from lichen and onto these backgrounds would compromise the efficacy of its camouflage, yet *D. atronivea* still prove difficult to detect to human observers. We therefore postulate that *D. atronivea* may incorporate masquerade as part of its defensive repertoire, such that the moth's colouration allows it to be disguised as a *distinct* patch of lichen, thereby maintaining the benefits of camouflage independent of background matching. Lichen masquerade has been purported in various groups, as mentioned above, yet to our knowledge this concept has not been formally tested. Here we applied the experimental approach developed by Skelhorn et al. (2010b) to explore this putative masquerade in *D. atronivea*. We pre-exposed naïve predators to unmanipulated and manipulated lichen models, as well as an empty arena, and subsequently recorded how they interacted with individual *D. atronivea*. We predicted that if the moths do benefit from masquerade, predators with previous experience of unmanipulated lichen should take longer to approach and handle the moths than chicks from the other treatments.

Methods

Moth and lichen collection

Declana atronivea moths (male and female) were collected at a light trap in Pureora Forest Park (−38.515408, 175.572307) and Tongariro National Park (−39.073694, 175.663864) during October and November 2019. Patches of white foliose lichen (made up of various species including *Xanthoparmelia scabrosa*, *Punctelia borreri*, *Parmelina labrosa*, *Parmotrema perlatum*, *Punctelia subrudecta*) that bore resemblance to *D. atronivea* were also collected.

Fig. 1 Male Declana atronivea moth. C. J Mark, 2019

2 cm

Chicken husbandry

Sixty-three female brown shaver chicks (*Gallus gallus domesticus*) were sourced from a commercial hatchery in Tuakau on day of hatch and immediately transported to the animal house facility at the University of Waikato in Hamilton. Forty-eight of these chicks were designated to the experimental treatments and housed in a large wooden pen ($120 \times 50 \times 50$ cm). The remaining 15 chicks were designated as 'buddy chicks' and housed in a separate, smaller cardboard pen ($90 \times 40 \times 40$ cm). White laminated cardboard was laid out on the floor of the pens with newspaper placed on top. The newspaper was changed three times a day due to soilage. All chicks were kept in a temperature and light controlled room maintained at 25–28 °C with a 14:10 h light:dark cycle using an air-conditioning unit and uncovered florescent lights with full daylight spectrum. The chicks were given ad libitum access to food (Topflite chick starter crumble) and water, except during training and experimental trials when they were temporarily food deprived for 30 min (in accordance with Animal Ethics regulations). The testing chicks were also provided with mealworms (*Tenebrio molitor*) twice a day. The chicks were left to acclimatise to the housing area for the first two days and were checked regularly to ensure they were consuming food and water, to change any soiled bedding, and to assess their general welfare.

Chicks were colour coded for identification using pipe cleaners (chenille sticks). Pipe cleaners were used as they are easy to mould and place onto the chicken's feet without causing stress and leave enough room for their feet to grow without becoming too tight. The pieces of pipe cleaner were cut to approximately 2.5 cm long and first wrapped around a pen to get the correct shape so that it could be slipped easily onto the chick's foot. The bands were then pressed on gently to tighten. The pipe cleaner colours were used to denote the group allocation and experimental treatment of the chicks (placed on the right foot) and their individual identity (left foot).

Training

On the third and fourth day, the 48 testing chicks were trained to eat starter crumbs from the floor of an experimental arena. The arena consisted of a wooden pen identical to that of the housing area with a $20 \times 50 \times 50$ cm section partitioned off using wire mesh to create a separate 'buddy arena' which was visible to the testing chicks in the experimental area (Fig. 2). Two 'buddy' chicks were placed in this buddy arena during all training and experimental trials to reduce any potential stress experienced by the testing chicks when placed alone in the arena. The buddy chicks were randomly chosen from the 15 individuals and rotated out every four trials. The training consisted of six trials per chick carried out over the two days (three trials per day). During the trials, starter crumbs were scattered across the arena floor and chicks were then placed in the arena for three minutes and allowed to explore and eat the food. For the initial two trials, the chicks were placed in the experimental arena in groups of three; then in groups of two; then in the final two trials they were placed individually in the arena. The rationale for training the chicks in progressively smaller groups was to gradually get them familiar with being in the arena on their own and to ensure they were comfortable with the surroundings and able to actively forage. By the end of the training trials, all chicks were eating crumbs from the arena floor.

Fig. 2 Experimental arena set-up with partitioned 'buddy arena'

Experience manipulation

To be able to misidentify masquerading prey as the object that they resemble, predators must first have had experience with that model object (Skelhorn et al. 2010b). The rationale behind the following trials was to manipulate the experience of naïve chicks to the putative masquerade models by exposing them to different stimuli and then observe how they interact with the prey in a final testing trial.

On the fifth and sixth day, the testing chicks were divided into six groups of eight individuals. Two groups were presented with a lichen patch (approximately 20 cm × 7 cm); two groups were presented with manipulated lichen (an otherwise similar lichen patch wrapped in blue wool to change its visual appearance while keeping the structure and odour the same, allowing us to test whether the benefit of masquerade depends on chicks having previous experience with normal looking lichen that the moths supposedly resemble); and two groups were placed in an empty arena (Fig. 3). The lichen patches were placed in the centre of the arena and chicks were individually introduced at the opposite side of the arena to the buddy chicks and facing the stimulus. Each chick underwent four separate two-minute
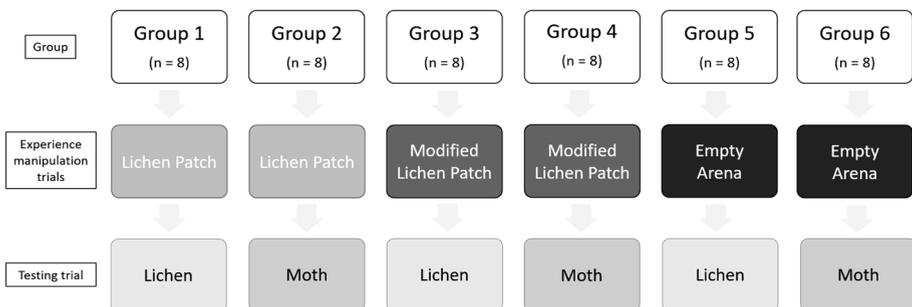
Fig. 3 The testing chicks were organised into six groups of eight. During the experience manipulation trials, chicks from groups 1 and 2 were placed in the arena with a lichen patch, chicks from groups 3 and 4 were placed in the arena with a modified lichen patch, and those form group 5 and 6 were presented with an empty arena. In the final testing trial, one group from each experience manipulation trial regime were presented with a small piece of lichen, and the rest were presented with a dead D. atronivea moth

trials. Chicks were trained in random order and were food deprived for 30 min prior to entering the arena. The trials were carried out over two days (two sets of trials per day).

A total of 32 lichen patches were used for the experience manipulation trials. They were split into 8 groups of 4 (accounting for the 8 individuals within each experimental group, and the four trials they each received). Each group of lichen were used 4 times (once across each of the four experimental groups that received a lichen or manipulated lichen stimulus) and no chicks in the same experimental group were presented with the same patch of lichen.

Post-experience tests

A single and final testing trial was carried out on day seven. The testing chicks were placed in the experimental arena for two minutes and presented with a test stimulus, either a dead *Declana atronivea* moth (that had been pinned out in a natural resting posture and dried one month prior) or a similarly sized small piece of lichen (approx. 4 cm×2.5 cm). One group from each of the three experience manipulation treatments (lichen, modified lichen, and empty arena) received a moth, and one group from each received the small lichen patch (see Fig. 3 for experimental design). The stimuli were positioned 15 cm away from the buddy arena and 25 cm away from the arena walls. The chicks were placed in the arena 15 cm away from the stimulus (30 cm away from the buddy arena) and facing towards the stimulus. The chicks were once again food deprived for 30 min prior to entering the arena. A different moth or lichen piece was used for each chick encounter. The latency to first peck at the stimulus was recorded, as well as the handling time, number of pecks, and whether the stimulus was consumed. Chicks that did not peck at the stimuli were recorded as having a latency of 125 s to simplify analyses.

Statistical analysis

We used negative binomial generalised linear regression models (GLM) to test whether chicks trained with unmanipulated lichen would take longer to attack the moth and handle the moth more cautiously (lower number of pecks and handling time), than chicks trained with manipulated lichen and the empty arena. Each response variable (latency, number of pecks, and handling time) was fitted in a separate GLM with negative binomial errors to determine if there were any differences among the groups in terms of each respective response. Subsequently, a likelihood ratio test was performed to calculate an overall p-value for the group term. Analyses were done using the packages "glmmTMB" (Brooks et al. 2017) and "lmtest" (Zeileis and Hothorn 2002) in R 3.6.3 (R Core Team 2020).

Results

The latency (in seconds) of chicks to attack the test stimuli did not differ between the experimental groups in the final testing trials (likelihood ratio test: $df=5$, $\chi^2 = 0.661$, $P=0.985$; Fig. 4a). Similarly, there was no significant difference in the number of pecks at the stimuli (likelihood ratio test, $df =5$, $\chi^2 = 2.499$, $P=0.776$; Fig. 4b), or the handling time (in seconds) (likelihood ratio test, $df =5$, $\chi^2 = 2.372$, $P=0.796$; Fig. 4c).
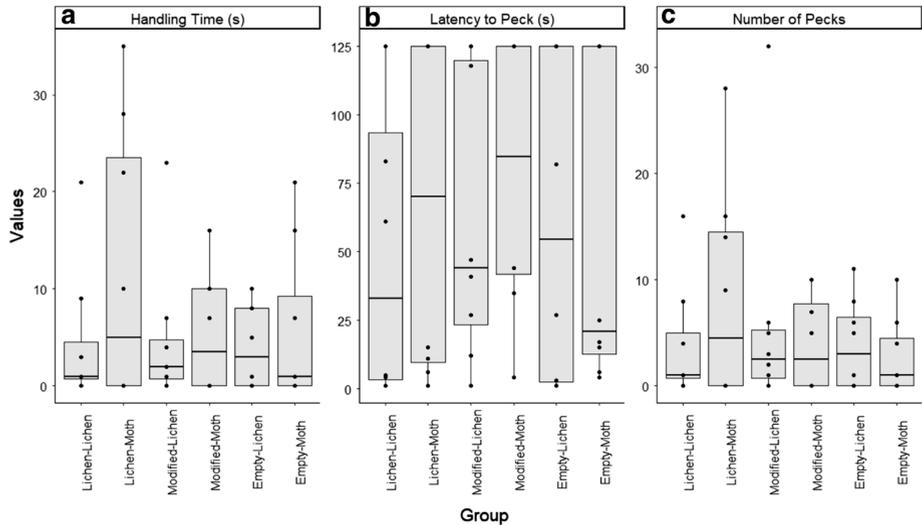
Fig. 4 Chick behavioural responses (**a** handling time (s); **b** latency to peck (s); and **c** number of pecks) to the different experimental treatments in the final testing trials

Discussion

Our results suggest that *D. atronivea* do not benefit from masquerade in the absence of a matching background. Following the experimental design from Skelhorn et al. (2010b), it was expected that if the moths do employ masquerade, chicks with previous experience of the unmanipulated lichen patches would take longer to approach and attack the moths and lichen stimuli than those chicks exposed to the modified lichen or empty arena. This is based on the hypothesis that the putative resemblance to lichen would promote misidentification by chicks who are familiar with lichen, causing them to not recognise the moths as a potential food source. This was not the case; the chick predators did not demonstrate any significant difference in how they interacted with the moths regardless of their prior experience. This does not necessarily preclude that *D. atronivea* use masquerade as a camouflage strategy, but perhaps they only benefit from the misclassification when found in the appropriate background context (i.e. near lichen).

Alternatively, rather than resembling a distinct *object* from the environment (i.e. a patch of lichen), the black and white forewing patterns of the moth may instead represent a *sample* of the environment, thereby promoting concealment through background matching. Background matching occurs when the appearance of an organism tends to match the visual components (colour, pattern, luminance, texture) of one or more backgrounds. This makes it visually indistinct from its surroundings allowing it to 'blend in' and remain undetected by predators (Stevens and Merilaita 2011). Evidence for the adaptive value of background matching has been demonstrated across numerous systems as diverse as marine isopods (Hultgren and Mittelstaedt, 2015), mice (Vignieri et al. 2010), birds (Troscianko et al. 2016), and moths (Walton and Stevens 2018). In these studies, animals which possessed colouration and patterning that more closely resembled their surrounding environment were found to have a greater likelihood of survival through reduced risk of detection, as measured via predator vision modelling or directly quantified with predation experiments.

To the untrained human eye, *D. atronivea* resting on lichen is virtually indistinguishable from its background substrate (pers. obs.), suggesting a likely role for background matching in the evolution of these visual signals.

An additional (though not mutually exclusive) hypothesis is that *D. atronivea* benefit from another camouflage strategy known as disruptive colouration, which functions via high contrast markings that intersect the edge of the body, creating false boundaries which hinder the ability of predators to detect or recognise a prey organism's true form (Stevens and Merilaita 2009a, b). The function of and mechanisms underlying disruptive colouration have been demonstrated in several studies (Cuthill et al. 2005; Merilaita and Lind 2005; Schaefer and Stobbe 2006; Stevens and Cuthill 2006; Stevens et al. 2006; Fraser et al. 2007; Webster et al. 2013; Kang et al. 2015; Price et al. 2019). It is possible that the black and white markings of *D. atronivea* serve to break-up surface continuity and obscure the moth's body outline thereby promoting concealment through disruptive colouration (Sharell 1971). Evidence suggests that disruptive markings may confer a survival advantage even if some pattern or colour elements are non-matching to the background (Schaefer and Stobbe 2006; Webster et al. 2013), potentially allowing prey to exploit more environments, thus improving survival even on backgrounds with which they only have a partial resemblance (Stevens et al. 2006). This may explain how *D. atronivea* remain difficult to detect on non-lichen backgrounds. One noted constraint of disruptive colouration is that contrasting pattern elements are often symmetric in nature, potentially reducing the efficacy of the camouflage (Cuthill et al. 2006a, b). Interestingly, *D. atronivea* possess asymmetric pattern elements (Fig. 1; pers. obs.) which further suggests potential for a disruptive effect of this moths' colour pattern. Lastly, disruptive colouration may work in conjunction with background matching through the sub-principle of differential blending whereby, in addition to the contrasting elements, some colour patches of the body blend into the background to further impede the detection of shape (Stevens and Merilaita 2009a, b).

Conclusion

We investigated lichen resemblance in *D. atronivea* and tested whether the putative lichen masquerade can function out of context and retain the benefits of camouflage independent of a matching background. Our results did not support this hypothesis; however, it is still possible that in natural conditions, with lichen at least present in the general habitat, *D. atronivea* benefit from masquerade when close to patches of lichen. Furthermore, observations of colour pattern elements, along with their apparent similarity to lichen backgrounds, may point towards other potential camouflage mechanisms in this species. It is possible that when it comes to resembling non-discrete objects such as lichen, there may be greater selection pressures to evolve cryptic strategies (i.e. background matching and disruptive colouration) rather than masquerade. *Declana atronivea* presents a good opportunity to develop our understanding of the interrelation between multiple mechanisms of camouflage and environmental context.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval This research was approved by the University of Waikato Animal Ethics Committee (Protocol No. 1076) and conducted according to the guidelines set out by the Code of Ethical Conduct of the University of Waikato and in compliance with the Animal Welfare Act 1999. All chicks were rehomed after this study.

Consent to participate Not applicable.

Consent for publication All authors consent to this research being published.

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