Animal Behaviour 163 (2020) 61–72

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Innovation and decreased neophobia drive invasion success in a widespread avian invader

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ARTICLE INFO

Article history:
Received 17 June 2019
Initial acceptance 18 September 2019
Final acceptance 23 January 2020

MS. number: 19-00417R

Keywords:
adaptive flexibility hypothesis
behavioural flexibility
common myna
innovation
invasive species
neophobia

Certain behavioural traits, including innovation and reduced neophobia, may facilitate successful invasions by allowing first arrivals to overcome the challenges of a novel environment. However, the extent to which these traits occur in invasive populations in comparison with native populations, and whether these traits' prevalence remains consistent throughout a species' introduced range, have been scarcely investigated. We tested whether object neophobia, food neophobia and two levels of motor innovation in the common myna, *Acridotheres tristis*, a widespread avian invader, in its native range (India) as well as across an invasive range (Israel), are more prevalent at the edge of the invasion front relative to its centre and to the native ranges. We found that individuals from the invasion front were more innovative and more tolerant of novel food than those from both nonfront invasive populations and the native range. Moreover, these traits showed a gradual loss within the invasive population with increasing time since population establishment. Our results provide crucial empirical evidence to support the adaptive flexibility hypothesis for invasion processes and emphasize the role of behaviour in biological invasions.

Successful invasions have been theorized to be mediated by various contributing factors, such as advantageous specificity and variation in genetics, morphology, life history traits and certain behavioural features (Juette, Cucherousset, & Cote, 2014; Mery & Burns, 2010; Shine, Brown, & Phillips, 2011; Wright, Eberhard, Hobson, Avery, & Russello, 2010). Among the behavioural traits thought to mediate the successful spread of non-native organisms into novel habitats and/or geographical ranges (i.e. biological invasion) are those that enable them to overcome the previously unmet challenges in the new environment. Several studies have shown the presence of either a single or a suite of unique or more prevalent behavioural traits in populations found at the front of the invasions (i.e. the 'front' population), relative to those populations in the native range or at nonfront sites of the invasion. These studies include birds (Liebl & Martin, 2014; Martin & Fitzgerald, 2005), amphibians (Candler & Bernal, 2015; Gruber, Brown, Whiting, & Shine, 2017a, 2017b, 2018; Gruber, Whiting, Brown, & Shine, 2017, 2018) and fishes (Myles-Gonzalez, Burness, Yavno, Rooke, & Fox, 2015). Wright et al. (2010) formulated the 'adaptive flexibility hypothesis', according to which the prevalence of behavioural plasticity decreases with time once the invasion has occurred, suggesting that traits that are beneficial in novel environments may become diluted or disappear in nonfront populations. This may occur since some traits stop being advantageous once the environment is no longer new, and can even be costly (Wright et al., 2010).

Among the behavioural traits that may facilitate invasion are reduced neophobia (i.e. less aversion towards a novel food item, object or place; Greenberg, Reader, & Laland, 2003), and greater innovation (i.e. more or swifter adoption of behaviours that allow the exploitation of previously unused resources or familiar resources in a new way; Greenberg et al., 2003). For example, in invasive populations of house sparrows, *Passer domesticus*, birds that originated from an actively invading population were faster to approach and consume novel food than individuals from an established population (Liebl & Martin, 2014; Martin & Fitzgerald, 2005). The benefits of a reduced neophobic response to a novel object or food item can include increased survival and reproduction (Sol, Timmermans, & Lefebvre, 2002), as individuals that persist better in a new environment by having a propensity for consuming novel foods may also pass that trait on to more offspring (Martin & Fitzgerald, 2005). Additionally, cognitive innovation has been

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https://doi.org/10.1016/j.anbehav.2020.02.012
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hypothesized to play a role in invasion success (Griffin, Diquelou, & Perea, 2014; Sol et al., 2002; Sol, Griffin, & Bartomeus, 2012), by increasing an individual's foraging potential and, therefore, improving its survival (Griffin et al., 2014; Sol, 2003). Innovation is traditionally divided into ‘consumer innovation’ (the willingness to eat new food) and ‘motor innovation’ (developing a new foraging technique; Sol et al., 2012). Although it is tempting to assume that there is a set of traits shared by successful invaders, for example that they present with decreased neophobia as well as with increased consumer or motor innovation, the relationship between the different behavioural suites remains unclear (Lermite, Peneaux, & Griffin, 2017; Sol, Griffin, Bartomeus, & Boyce, 2011).

One of the ways to test the role of behaviour in invasion success is to explore the expression of the hypothesized pattern of behavioural traits across different stages of the invasion process in a successful invader. A suitable candidate for this approach is the common myna, *Acridotheres tristis*, a widespread avian invader native to south Asia and the Indian subcontinent that has been introduced to, and has successfully invaded, almost every continent in the world. Indeed, it is considered one of the ‘100 worst invasive alien species’ (Lowe, Browne, Boudjelas, & De Poorter, 2000; Magory Cohen, McKinney, Kark, & Dor, 2019). The species has been found to be capable of solving high-level innovation tasks (Griffin & Diquelou, 2015; Griffin et al., 2014; Griffin, Guez, Lermite, & Patience, 2013; Lermite et al., 2017; Sol et al., 2011), and was flexible in its range of responses to novel objects and food (Sol et al., 2011). Many of the common myna invasive populations are still expanding, creating an opportunity to observe the prevalence of these traits in truly novel environments (i.e. the active invasion fronts). One such location is Israel, to which the species was introduced in 1997 (Holzapfel, Levin, Hatzofe, & Kark, 2006), and where its range is still expanding (Magory Cohen et al., 2019).

To estimate the role of neophobia and motor innovation in invasion success, we studied these traits in wild-caught common mynas from an invasive population in Israel (at the invasion fronts and from nonfront sites) and from populations in its native range in India. By conducting a series of behavioural tests for each subject, we sought to describe the frequency of these behavioural phenotypes as a function of the population type (i.e. ‘native range’ and each of the invasion stages, ‘front’ and ‘nonfront’). These tests were designed to parallel the novel challenges met by invading individuals arriving at new environments, such as encountering unknown objects, the necessity to feed from unfamiliar food resources, and the need to obtain foods through new foraging motor patterns and techniques to access them. We hypothesized that birds caught at the invasion front would be less neophobic to both novel objects and food and would display a higher propensity to innovate. In turn, according to the adaptive flexibility hypothesis (Wright et al., 2010), we expected that these traits would become diluted (i.e. diminished) in the population in time, so that as more time passes after the arrival of the first invaders the prevalence of these hyperplastic phenotypes would decrease. By investigating the frequency of these traits among replicate sites found at the different stages of the invasion process in the Israeli population, we aimed to further test the role of behavioural plasticity in facilitating biological invasions.

METHODS

Animal Capture and Care

We trapped a total of 120 invasive common mynas (31 juveniles and 89 adults) at different locations along the invaded range in Israel (eight locations) and 25 native birds (one juvenile and 24 adults) in India (representing the historically native range; two locations; Fig. 1, Table A1). We determined the age of the birds by identifying moulting patterns, which differentiate between juveniles and adults following one complete moult prior to the first breeding season of an individual as an adult in common mynas (Cramp & Perrins, 1994). In the absence of clear criteria defining front and nonfront populations, we considered areas in which common mynas have more recently arrived as front populations. This definition maintained the novelty of the new environment but also relied on the bimodal distribution of our own population establishment data to determine a biologically relevant cutoff value (<5 years; Fig. A1). Because of the difficulty in defining front populations, we also analysed the introduced population using a continuous measure that proxied the population type (‘years since introduction’ and ‘distance from source’; see Statistical Analyses). We obtained information regarding the time of invasion from a combination of sources including the Israel Nature and Parks Authority and a citizen science project executed in Israel for a study published elsewhere (Magory Cohen & Dor, 2019). In addition, we recorded the breeding status (breeding/nonbreeding) for each bird according to the time of capture (Cramp & Perrins, 1994).

All birds were trapped in urbanized areas in disturbed habitats. Birds were captured using modified specialized myna traps (Tidemann & ANU Fenner School, 2009) and ‘bucket’ traps (both considered to require some boldness), and a few by opportunistic mist-netting sessions. Because the number of opportunistic trappings was very small (up to two in each population type), we did not include this factor in the analyses. Capture sessions were conducted between October 2016 and March 2018 in Israel, and between September 2017 and March 2018 in India. Birds were subsequently brought into captivity and housed in individual cages, 1 × 1 m and 1 m high, at the Zoological Research Garden at Tel Aviv University (Israel) and at the Wildlife Institute of India in Dehradun (Uttarakhand). All cages contained a nestbox, one or two perches, a watering/bathing bowl and a feeding dish. Whenever the number of birds caught exceeded the number of available cages, the remaining birds were housed together in a 3 × 4 m and 2 m high transition cage (Israel). Mynas were given ad libitum access to food, which included either a mixture of grains (mixture 1: barley, wheat, corn, soy cusps, sunflower cusps), a mixture of grains and dog pellets (mixture 2) or a mixture of durum wheat, cooked white rice, Gaattiya (Indian snacks made for human consumption from chickpea flour) and baked bread (mixture 3), based on preliminary food preference trials (Table A1). Birds were also supplemented with live mealworms.

Blood was taken from the brachial vein and stored in a lysis buffer (modified from White & Densmore, 1992) to determine the genetic sex of the bird (see below). Morphometric measurements were recorded to an accuracy of 0.1 mm, but they were not subsequently used in this study. Birds were allowed 48 h of acclimation before the first behavioural test was conducted. Once the experiments were completed (4 days), subjects were transferred to the Israeli Nature and Parks Authority (permit numbers 2015/40828 and 2017/41780; because as an invasive species, they were not allowed to be returned to nature in Israel). In India, subjects were banded and released at their capture site. All animal care, husbandry and experimental procedures followed the ethical guidelines of the Tel Aviv University ethics committee (permit numbers L-15-033 and 04-17-056), and the Wildlife Institute of India Animal Welfare committee and Uttarakhand State Forest Department (permit L. No. 1258/5–6).

General Procedures

Each bird underwent four consecutive behavioural tests in a fixed order which included object neophobia (day 1), food

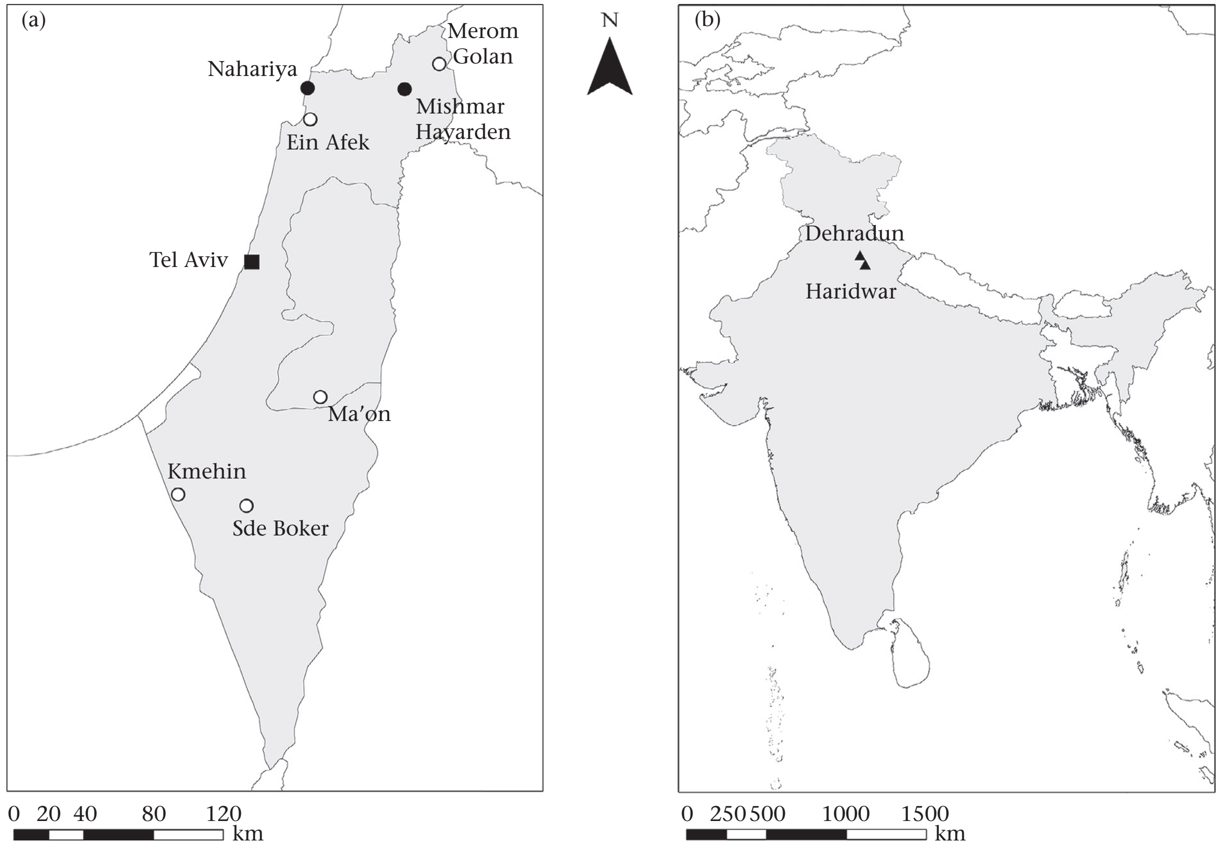

Figure 1. Sampling locations used in this study. (a) Sampled common myna populations in Israel. Black square: point of introduction in 1997; black circles: nonfront locations; white circles: invasion front locations. (b) Sampled common myna populations in India (native range).

neophobia (day 2), easy motor innovation (day 3), and difficult motor innovation (day 4; Fig. 2). Some procedural modifications were made throughout the study to improve the tasks (e.g. adding a more difficult innovation task); therefore, the sample sizes differed between the behavioural tests following the exclusion of birds that did not engage in the finalized version of the task (Table A2). The order of the experiments was held fixed to avoid gradual habituation to the novel stimuli (Sol et al., 2011). All experiments were recorded on video as well as observed from behind a blind to minimize the effect of the presence of the observer. Video recordings were analysed blindly with regard to the origin of the individual (front, nonfront or native).

Before each experiment, birds were food deprived overnight, with an additional 3.5–4.5 h of daylight added either before, after or both so that total daylight deprivation time did not exceed 4.5 h in the hours prior to the experiment. Once the experiment was concluded, ad libitum access to food was re-established until the beginning of the food deprivation period for the next trial. All four experiments included a control phase of a maximum of 20 min followed by a test phase of an additional maximum of 20 min. In cases where the bird had not completed the control phase within

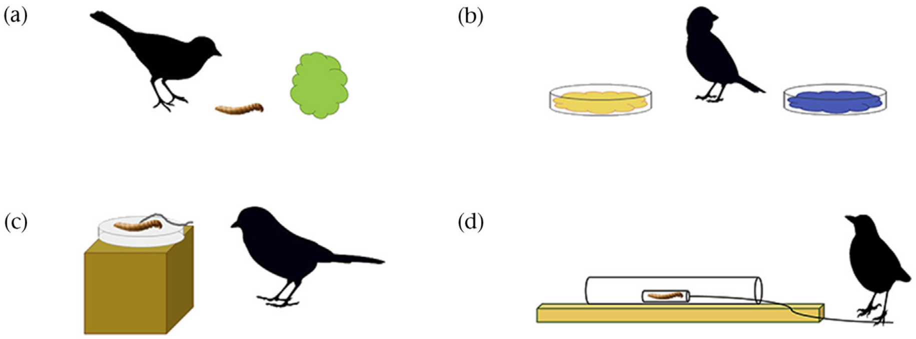

Figure 2. Schematic illustration of behavioural tasks used in the study. (a) Object neophobia task, in which the foreign object was an amorphous, green, semi-inflated ball. The mealworm was placed beside it, ca. 5 cm away. (b) Food neophobia task, in which the novel food was regular food dyed blue. The foods were not presented simultaneously to the bird, see text for details. (c) Motor innovation (easy) task, in which a mealworm was placed inside a closed Petri dish to which a string was attached. Birds had to lift the lid to feed. (d) Motor innovation (difficult) task, in which a mealworm was placed in a closed 1.5 ml tube attached to a long string within a long clear plastic tube. Birds had to pull the string until the 1.5 ml tube came out of the plastic tube.

20 min, the bird was allocated a capped time of 1201 s, which marks the end of the experiment without solving. Birds that solved the motor innovation tests were tested again after a minimum of 30 min to confirm that success was achieved intentionally and not by chance, but only the first measurement was used in the analysis.

Behavioural Tests

Object neophobia test

We tested neophobia to a foreign object via a standard test in which the object is placed near the feeding apparatus in the cage (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sol et al., 2011). The object we used was an amorphous semi-inflated green rubber ball, approximately 10 cm in diameter (Fig. 2a). This uncommon shape gave us confidence that the birds were unlikely to have encountered a similar object in nature. The control phase included presenting the mynas with a mealworm placed in the feeding apparatus. Once the myna had consumed the food, the observer left the blind, inserted another mealworm into the food apparatus and placed the green object next to it approximately 5 cm apart, thus initiating the test phase. The observer then returned to behind the blind and the trial starting point was determined as the moment the observer was no longer within the recording camera's frame. An adjustment was made to the protocol after several trials showed that mynas failed to complete the control phase because of fear of the presence of the observer, encountered for the first time. Therefore, we added an additional control step preceding the control phase, in which a mealworm was placed inside the food apparatus and excluded the previous trials from the analysis. This step minimized the aversive response towards the observer, and improved mynas' responsiveness in the control phases. We estimated the performance of each individual by subtracting the latency to feed during the control phase from the latency to feed during the test phase.

Food neophobia test

We tested neophobia to novel food (also referred to as ‘consumer innovation’; Sol et al., 2011) by using a blue-coloured component of the regular feed (in Israel: mixed grains; in India: cooked rice). We chose to use the exact same food type in control and treatment to avoid bias created by food preferences that stems from irrelevant attributes such as consistency, piece size and shape, and we coloured the food with a blue nontoxic dye because blue food is relatively rare in natural environments, thus lowering the chance of previous familiarity with it (Fig. 2b). We used different food in Israel and in India because preliminary food preference tests suggested that Israeli mynas do not readily consume cooked rice whereas Indian mynas do not readily consume grains, which also led to the elimination of both components from the regular ad libitum feed, respectively (see above). The control phase included presenting the myna with the untreated food. Once the myna had clearly begun to eat the food, the observer left the blind and replaced the regular food with the blue-coloured food, thus initiating the test phase. Mynas were only allowed to consume the regular food briefly before initiating the test phase. The observer then returned to behind the blind and the trial starting point was determined as the moment the observer was no longer within the recording camera's frame. We estimated the performance of each individual by subtracting the latency to feed during the control phase from the latency to feed during the test phase.

Motor innovation tests

We applied two tests with increasing level of difficulty to examine motor innovation in mynas. The first included a puzzle box made of a 10 cm diameter Petri dish fixed to a wooden cube, with the smaller lid placed on top so that the birds could see the food placed inside (hereinafter: ‘petri test’). A small hole was pierced in the lid through which a string was fitted, which had to be lifted to reach the food placed inside the Petri dish (Fig. 2c). The control phase included a mealworm placed inside the Petri dish with the lid open and placed next to the wooden box. The preferred (mealworm) food was placed inside the open Petri dish rather than in the regular food apparatus to reduce the neophobic response to the apparatus itself. Once the myna consumed the food, the observer left the blind, placed another mealworm inside the Petri dish and closed the lid, thus initiating the test phase. The observer then went back behind the blind and the trial starting point was determined as the moment the observer was no longer within the recording camera's frame.

The second motor innovation test was more complex and predicted to be harder to solve. It consisted of a 30 cm long clear plastic tube fixed on a 42 cm long wooden board; a 1.5 ml clear tube, containing the mealworm, attached to a 40 cm long string was placed either next to the tube (control phase) or in the middle of it (test phase; hereinafter: ‘tube test’; Fig. 2d). During the control phase, the 1.5 ml tube was left open so that the bird could consume the food, and placed on top of the wooden board next to the large tube to reduce any neophobic response to the apparatus itself. For the bird to succeed in solving the task, it needed to pull the string horizontally until the 1 ml tube containing the mealworm was outside the plastic tube. Since the mealworms escaped the 1.5 ml tube when it was open, we kept it closed during the test phase; once a bird succeeded in pulling the thread so that the 1 ml tube was within reach, the observer then opened it, allowing the bird to consume its reward.

In both innovation tests, we recorded both the latency to touch the apparatus with the beak and the latency to solve the task and estimated the performance of each individual by subtracting the latency to feed during the control phase from the latency to feed during the test phase.

Sex Identification

We extracted DNA from the blood samples by using the gSYNCTM DNA Extraction Kit (Geneaid Biotech Ltd., Taiwan). We amplified sex identification regions on the Z (male and female) and W (female only) avian sex chromosomes with the primers F2250 and R2718 (Fridolfsson & Ellegren, 1999) or CHD1-i16-F and CHD1-i16-R (Suh, Kriegs, Brosius, & Schmitz, 2011). The 25 μl volume solution used for PCR comprised 3 μl of DNA extract, 2.5 μl of 10X-PCR buffer, 2.5 μl of 0.2 mM dNTPs, 2.5 μl of 20 mM $MgCl_2$, 0.5 μl of forward and reverse primers (10 mM) and 0.5 Units/reaction of Hy-Taq DNA Polymerase (Hylabs, Rehovot, Israel). The PCR cycles comprised an initial denaturation step at 94 °C for 2 min followed by a total of 35 cycles of 30 s at 94 °C, 1 min at annealing temperature and 1 min elongation at 72 °C, with a final extension time of 10 minutes at 72 °C. Annealing temperatures were 48 °C and 52 °C, respectively. PCR products were run on 1.5% agarose gel and visualized to determine band separation(s) and the indicated sex of the bird.

Statistical Analyses

We aimed to model task-solving success for both neophobia and innovation tests primarily as a function of the population type (native, nonfront or front), which we further divided according to two main factors in the invasive population: years since the invasion and distance from the invasion source. We used a Fisher's exact test to compare the proportions of individuals that solved the tasks, between the different population types. For parametric tests, we assessed the normality of the data by employing Shapiro - Wilks normality tests. We searched for potential correlations between explanatory variables by using the Pearson correlation coefficient test ($r > 0.5$). Models were first run with the full data set of individuals from both India and Israel with population type as a categorical predictor variable (native, front and nonfront) because continuous estimators could not quantify native birds in terms of distance from source or years since invasion. Additional explanatory variables that may affect individual performance were also included (sex, age, feed type and breeding status).

Subsequently, we also analysed a subset of the data that included sites from only the invasive population (Israel). Continuous variables were standardized by subtracting the mean and dividing by the standard deviation using the ‘stdize’ function in R package ‘pls’ version 2.7–0 (Mevik & Wehrens, 2007). In addition, we included two random factors of feed type and the identity of the observer. We modelled three different response variables: the latency to solve the task, the outcome of the test (success/failure) and the latency to touch the apparatus (innovation tasks only). Because response variables that were capped at 20 min (latency to touch or solve) should be treated as censored data (Lermite et al., 2017; Liebl & Martin, 2014; Sol et al., 2011), we applied Cox proportional hazards models to model these variables using the ‘coxme’ R package (Therneau, 2018).

Additionally, we used general linear mixed models to model the outcome (family = binomial, link = probit), for which we assessed the goodness-of-fit by measuring marginal R squared (for fixed variables) and conditional R squared (for all variables). To select the best model, we ran all the possible models (including the null model) and selected the best models using the corrected Akaike information criterion (AICc; Symonds & Moussalli, 2011). We then employed model averaging over the best models (ΔAICc ≤ 2) using the R package MuMIn (Barton, 2018). To describe the statistical significance of the predictor variables, we calculated 95% confidence intervals (R Core Team, 2013). Because the numbers of juveniles were small and unequal across the population types ($N_{\text{Native}} = 1$, $N_{\text{Nonfront}} = 27$, $N_{\text{Front}} = 1$), we omitted juveniles completely from the AICc analyses.

RESULTS

Differences Between Invasive and Native Populations

The percentage of individuals that succeeded in solving the behavioural tasks differed significantly between tasks (Fig. 3, Table A2). The more seemingly difficult the task, the fewer individuals succeeded in completing it across all three population types (Table A2).

As predicted, we found significant differences between invasion front populations and native populations in food neophobia (odds ratio = 9.34, $P = 0.001$), in the easy motor innovation (odds ratio = 10.19, $P = 0.002$) and the difficult motor innovation tasks (odds ratio = 9.09, $P = 0.027$). In addition, nonfront populations and native populations differed significantly in the food neophobia task (odds ratio = 6.21, $P = 0.002$). Finally, in the easy motor innovation task (odds ratio = 3.85, $P = 0.013$), but not in the other tasks (object neophobia: odds ratio = 4.14, $P = 0.225$; food neophobia: odds ratio = 1.52, $P = 0.727$; difficult innovation task: odds ratio = 1.86, $P = 0.374$), nonfront populations also performed significantly worse than front populations.

When the nonsignificant population type patterns of object neophobia task were excluded, task-solving rates were highest in front populations, followed by nonfront populations, and were lowest in populations from the native range (Fig. 3, Table A2). All the birds that solved the difficult motor innovation task also solved the easy motor innovation task, and 92.86% of these succeeded at the object neophobia test, but only 88.10% also ate the blue-coloured food (food neophobia).

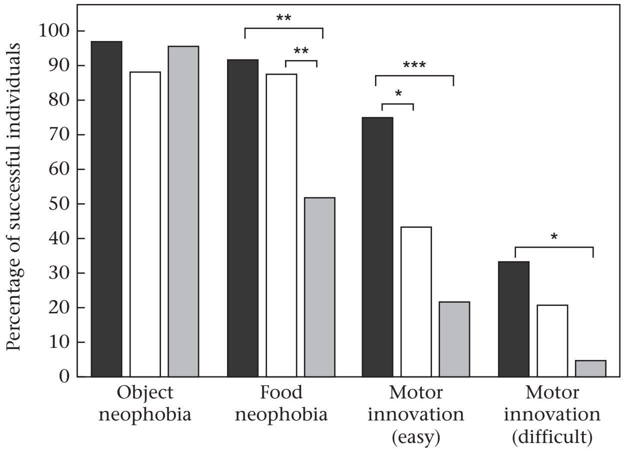

Figure 3. Differences in success rates of individuals in each of the behavioural tasks as a function of their population type. Black bars: invasion front; white bars: nonfront; grey bars native. Fisher's exact tests were conducted to test differences between population types. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

The most frequent statistically significant explanatory variable in the best models for neophobia and motor innovation was population type (Table 1). It explained the latency to solve the task, the latency to touch the apparatus and the outcome, mostly as a sole explanatory variable. Individuals from the front population type were more likely to succeed in solving the motor innovation tasks and the food neophobia task than those from the native or the nonfront population types (Table 1). However, an additional factor, breeding status, also explained the model in the food neophobia task (Table 1). In addition, the latency to solve the food neophobia and motor innovation tasks was longer for birds from the native than the front population type (Table 1, Fig. 4b, c, d). Additionally, birds from native populations were slower to touch the apparatus in the easy motor innovation task ((Table 1). No predictor variables significantly explained the results of the object neophobia test (Table 1, Fig. 4a).

Differences Within an Invasive Population

When modelling the invasive population sites alone, we replaced the categorical explanatory factor of ‘population type’ with continuous measures of the number of years since the invasion and the distance from the source of the invasion. Since the factors ‘years since invasion’ and ‘distance from source’ were significantly positively correlated (object neophobia: Pearson $r = -0.62$, $P < 0.001$; food neophobia: Pearson $r = -0.62$, $P < 0.001$; easy motor innovation: Pearson $r = -0.58$, $P < 0.001$; difficult motor innovation: Pearson $r = -0.58$, $P < 0.001$), the latter was removed from the models. The patterns observed in the comparison between all three population types were partially repeated when only individuals from the invasive range were modelled and continuous variables were used to quantify invasion parameters, although null models were the best models for most of the dependent variables that were tested (Table 2). We found that the number of years since invasion varied significantly negatively with the latency to touch the apparatus in the easy motor innovation test, and the outcome to a lesser degree, so that the more years that had passed since the arrival of the first birds, the lower the probability of solving the task and the longer the latency to make first contact (Table 2). Additionally, when the birds were not breeding,

Table 1
Cox proportional hazard models and general linear mixed models relating components of behavioural tasks to population type and a series of confounding explanatory variables between invasive and native populations

Task	Response	Model type	Explanatory variables included in the best model	Estimate/ coefficient	SE	z/t	P	Confidence interval (2.5%, 97.5%)		R^2(m)	R^2(c)
Object neophobia	Outcome	glm (family= binomial (link=probit))	No predictors were statistically significant								
	Latency to solve	Cox proportional hazard	No predictors were statistically significant								
Food neophobia	Outcome	glm (family= binomial (link=probit))	Breeding status (not breeding)	0.83	0.35	2.33	0.020	0.13	1.53	0.28	0.30
			Population type (native)	−1.18	0.47	2.47	0.013	−2.12	−0.25		
	Latency to solve	Cox proportional hazard	Population type (native)	−1.22	0.48	2.53	0.012	−2.17	−0.27		
Motor innovation (easy)	Latency to touch	Cox proportional hazard	Population type (native)	−2.05	0.76	2.70	0.007	−3.54	−0.57		
			Population type (nonfront)	−0.83	0.35	2.34	0.019	−1.52	−0.13		
	Outcome	glm (family= binomial (link=probit))	Population type (native)	−1.43	0.42	3.32	0.001	−2.27	−0.58	0.25	0.25
			Population type (nonfront)	−0.79	0.37	2.10	0.036	−1.53	−0.05		
	Latency to solve	Cox proportional hazard	Population type (native)	−1.52	0.53	2.89	0.004	−2.55	−0.49		
			Population type (nonfront)*	−0.64	0.34	1.88	0.060	−1.31	0.03		
Motor innovation (difficult)	Latency to touch	Cox proportional hazard	No predictors were statistically significant								
			Population type (native)*	−2.14	1.18	1.82	0.069	−4.44	0.17		
	Outcome	glm (family= binomial (link=probit))	Population type (native)	−1.42	0.59	2.38	0.017	−2.59	−0.25	0.25	0.25
	Latency to solve	Cox proportional hazard	Population type (native)	−2.38	1.07	2.23	0.026	−4.47	−0.29		

Task components included task outcome and latency to solve the task (all models) as well as latency to touch the apparatus (motor innovation models). All models were conducted with breeding status, population type and sex as fixed factors and observer ID and feed type as random factors. Models were selected using the Akaike information criterion (AIC) and averaged over the best models ($\Delta AIC \leq 2$). Only significant predictor variables ($P < 0.05$) or variables approaching significance ($P < 0.1$) are shown. R^2(m): marginal R^2; R^2(c): conditional R^2.
*$P < 0.1$.

the probability of solving the test decreased in the difficult motor innovation task, but increased in the food neophobia task and the latency to solve it increased (Table 2). Males were also more likely to succeed in the food neophobia task than females (Table 2).

DISCUSSION

We have demonstrated that predictable behavioural population level differences exist between the invasive and native ranges of a widespread avian alien. Increased motor innovation and decreased food neophobia characterized those individuals that were captured in the introduced range relative to the native populations. Several of these behavioural differences were also observed in a graded fashion across different stages of the establishment age within the invasive populations, suggesting that these traits have become diluted as more years have passed since the arrival of the first invaders. Therefore, our data support the notion that motor innovation to explore foraging techniques and tolerance of novel foods contribute to the invasion success of common mynas.

Novel environments present new challenges for first invaders. Unfamiliar food resources necessitate the development of new behaviours for an animal to survive in a new environment, although it may come at a cost (Greenberg et al., 2003; Greenberg & Mettke-Hofmann, 2001; Griffin, Netto, & Peneaux, 2017; Ingley & Johnson, 2014; Sol et al., 2011). Similarly, innovation acts as an agent in solving new problems, thus increasing survival rates (Griffin & Guez, 2014; Griffin et al., 2017; Overington, Griffin, Sol, & Lefebvre, 2011; Sol, 2003; Sol et al., 2012; Sol, Uncan, Blackburn, Cassey, & Lefebvre, 2005). These traits have been hypothesized to increase invasion success by equipping invaders with advantageous abilities to overcome previously unmet obstacles (Juette et al., 2014; Sol et al., 2002). Invasive common mynas have been reported to be both innovative (Griffin & Diquelou, 2015; Griffin, Guez, et al., 2013; Griffin et al., 2013; Lermite et al., 2017; Sol et al., 2012) and displaying low levels of neophobia (Sol et al., 2011, 2012; but see Griffin & Diquelou, 2015), although these traits have never been tested in native common mynas or mynas at different invasion stages. Our results indicate that there are differences in the prevalence of these traits between populations originating in different population types (Fig. 3), and that individuals from invasive populations can be characterized with decreased food neophobia and increased motor innovation relative to native populations. While this study confirms previous findings in this species in a different invasive range (Australia: Griffin & Diquelou, 2015; Sol et al., 2012), it demonstrates that these traits are also not necessarily present throughout its full invasive distribution range (Fig. 4b, c, d, Table A2), thus emphasizing their importance in the invasion process. Additionally, in accordance with previous findings in wild-caught house sparrows (Martin & Fitzgerald, 2005) and cane toads, *Rhinella marina* (Gruber, Brown, et al., 2017b), no differences were found between populations in response to novel objects (Table 2). The fact that this trait also did not differ between native and invasive common myna populations (Table 1) suggests that it is as prevalent in the native range and

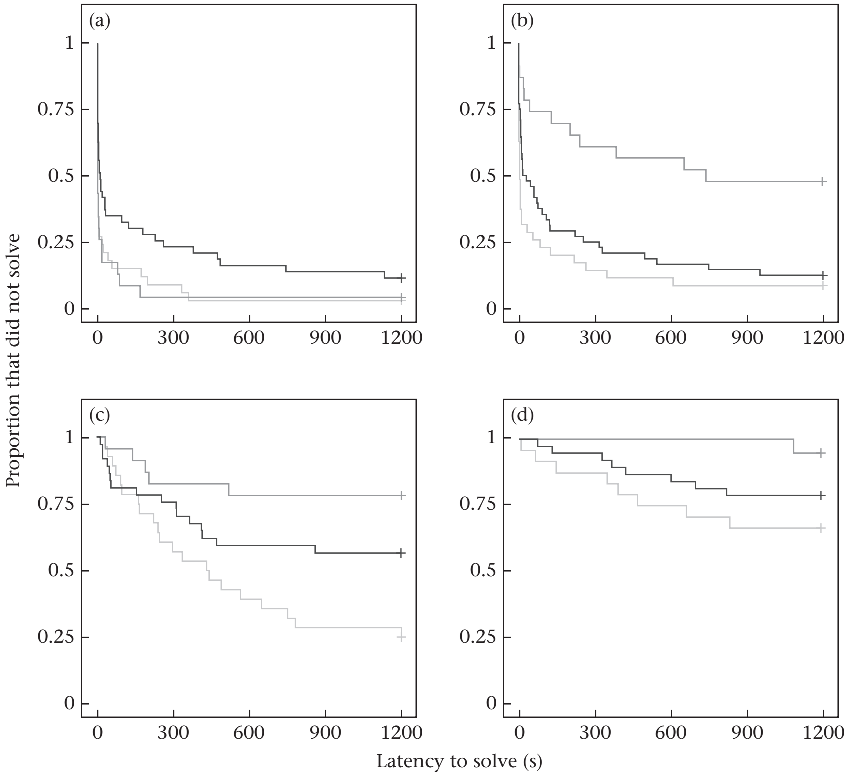

Figure 4. Differences in the latency to solve each of the behavioural tasks as a function of population type: (a) object neophobia; (b) food neophobia; (c) motor innovation (easy); (d) motor innovation (difficult). 'Survival' rates describe the proportion of the individuals that did not solve the task as a function of time (s). Light grey: invasion front; black: nonfront; dark grey: native. Figures were generated using the 'survival', 'ggplot2' and 'survminer' packages in R 26–28. (d) The second-best AICc model (see Table 1).

possibly less important during invasion. Although other factors also explained some of the responses (e.g. sex, breeding status: Tables 1 and 2), we suspect that they might reflect stochastic influences in specific variables and may not represent a consistent trend.

Empirical evidence supporting the assertion that traits that are advantageous during invasion do not remain constant, but become diluted and even lost with time, has only recently been obtained as within-population comparisons have been conducted

Table 2

Cox proportional hazard models and general linear mixed models relating components of behavioural tasks to population type and a series of confounding explanatory variables within an invasive population

Task	Response	Model type	Explanatory variables included in the best model	Estimate/ Coefficient	SE	z/t	P	Confidence interval (2.5%, 97.5%)		R^2(m)	R^2(c)
Object neophobia	Outcome	glm (family= binomial (link=probit))	No predictors were statistically significant								
	Latency to solve	Cox proportional hazard	No predictors were statistically significant								
Food neophobia	Outcome	glm (family= binomial (link=probit))	Breeding status (not breeding)	0.79	0.37	2.12	0.034	0.06	1.53	0.13	0.21
			Sex (male)	0.35	0.02	21.50	<0.001	0.32	0.39		
	Latency to solve	Cox proportional hazard	Breeding status (not breeding)	0.56	0.27	2.09	0.037				
Motor innovation (easy)	Latency to touch	Cox proportional hazard	Years since invasion (std)	−0.41	0.17	2.44	0.015	−0.73	−0.08		
	Outcome	glm (family= binomial (link=probit))	Years since invasion (std)*	−0.32	0.17	1.89	0.058	−0.66	0.01	0.13	0.23
	Latency to solve	Cox proportional hazard	No predictors were statistically significant								
Motor innovation (difficult)	Latency to touch	Cox proportional hazard	No predictors were statistically significant								
	Outcome	glm (family= binomial (link=probit))	Breeding status (not breeding)	−0.74	0.36	2.04	0.041	−1.45	−0.03	0.13	0.13
	Latency to solve	cox proportional hazard	No predictors were statistically significant								

Task components included task outcome and latency to solve the task (all models) as well as latency to touch the apparatus (motor innovation models). All models were conducted with breeding status, years since invasion and sex as fixed factors and observer ID and feed type as random factors. Models were selected using the Akaike information criterion (AIC) and averaged over the best models (ΔAIC ≤ 2). Only significant predictor variables ($P < 0.05$) or variables approaching significance ($P < 0.1$) are shown. (std): standardized; R^2(m): marginal R^2; R^2(c): conditional R^2.

*$P < 0.1$.

in invasive species. Differences between invasion front and nonfront ranges have already been documented for various behavioural traits such as food neophobia (Liebl & Martin, 2014; Martin & Fitzgerald, 2005; Pintor, Sih, & Bauer, 2008), boldness (Cote, Fogarty, Brodin, Weinersmith, & Sih, 2011; Gruber, Brown, et al., 2017b; Myles-Gonzalez et al., 2015), aggression (Duckworth & Badyaev, 2007; Suarez, Tsutsui, Holway, & Case, 1999) and exploration (Gruber, Brown, et al., 2017b; Liebl & Martin, 2012). Our results indicate that despite the relatively recent introduction of common mynas into Israel (ca. 20 years), the time that has passed since the arrival of the first invaders has been a significant (negative) predictor of increased motor innovation and decreased food neophobia, with the highest percentages of innovators and non-neophobic birds found at invasion fronts (Fig. 3, Table A2), despite receiving less support in the multivariate analyses (Table 2). These patterns are in agreement with the predictions of the adaptive flexibility hypothesis, which posits that traits that are no longer beneficial in an environment that is becoming familiar, especially when they may entail high risks and fitness costs, become less prevalent as time passes (Lee, 2011; Wright et al., 2010). However, the mechanism allowing for these differences to emerge remains unclear, and has been suggested to be the result of natural selection (Shine et al., 2011), spatial sorting (Lee, 2011; Shine et al., 2011) or behavioural plasticity (Mery & Burns, 2010; Pettit, Greenlees, & Shine, 2016). While a heritable component is required for both natural selection and spatial sorting to occur, behavioural plasticity describes a phenotypic variation within an individual in response to a change in complex environmental conditions (Mery & Burns, 2010). Recently, ambiguous evidence has accumulated to support both genetic and plastic scaffoldings for behavioural plasticity, either from studying candidate genes (Mueller et al., 2014) or from conducting common garden experiments (Atwell, Cardoso, Whittaker, Price, & Ketterson, 2014; Gruber, Brown, et al., 2017b; Pettit et al., 2016). While our results are correlational in their approach, and have limited relevance to interpreting the underlying mechanism, they provide invaluable evidence of the gradual outcome of the process as a once novel invasion front becomes a more and more familiar environment. Our results do not exclude complementary mechanisms, such as phenotype transfer through social learning, suggested as an alternative driver of behavioural plasticity by Wright et al. (2010). Social learning is an established mechanism in common mynas (Griffin, 2008; Griffin & Boyce, 2009; Hubbard, King, Vu, & Blumstein, 2015), and future research could benefit from testing the role of social learning in shaping behavioural diversity in introduced and native populations. Additionally, whether increased innovation and decreased neophobia increase fitness in the invasive range remains untested. Studies that compare these traits in introduced populations can provide additional support for the role of these traits in facilitating invasion.

Because of certain limitations during trapping procedures (e.g. lower bird densities in front areas, time-limited and finance-limited efforts in the native range), our study was geographically constrained to only two sites in the native range and to somewhat smaller sample sizes in the front than in the nonfront populations. In addition, the native range subject sample size was also smaller ($N = 24$) than for the front ($N = 36$) and the nonfront ($N = 49$) sites. While multivariate general linear mixed models are considered appropriate for unequal or blocked designs (Bolker et al., 2009; Chaves, 2010), we cannot exclude the possibility that by including additional sites in the native range or more introduced populations, our results might reflect a greater variance. Future efforts will benefit from expanding the sampling range to gain insight as to the full spectrum of the phenomenon described here. However, given the complexity of the behavioural tasks and the sufficient statistical power of our results to detect several significant results, we maintain that our study reflects a general pattern in the common myna that supports similar previous findings in this and other invaders (Pintor et al., 2008; Suarez et al., 1999).

Invasive species are considered the second most common threat associated with native species' extinctions (Bellard, Cassey, & Blackburn, 2016). By increasing our understanding of the behavioural attributes that facilitate successful invasions, we can improve mitigation strategies and control of unintentional introductions. Knowledge of characteristics of successful invaders such as the common myna can aid by extrapolating it to other potentially invasive species and thus advance the pre-emptive measures taken to prevent future invasions (Kolar & Lodge, 2001; Sol, 2003). Moreover, this information also highlights the invasive ability of common mynas and emphasizes this species' potential to establish and spread in any additional introductions, thus providing countries and mitigation authorities with crucial knowledge for determining the consequence of animal trade (Genovesi & Shine, 2004; Magory Cohen et al., 2019). Characterizing the behavioural profile of successful invaders also allows us to assess the possible impact on native species, although more work is needed (Chapple, Simmonds, & Wong, 2012; Juette et al., 2014; Rodriguez, 2006). In addition to practical implications, our work extends the knowledge of behavioural patterns observed over a native and an invasive range of an important global invader and provides crucial empirical evidence to support the adaptive flexibility hypothesis. These results are in agreement with the hypothesized role of behavioural flexibility in invasion success and offer an exciting opportunity to harness this knowledge for future efforts in understanding successful biological invasions, including the neurogenomic and cognitive underpinnings of behavioural flexibility and innovation.

Acknowledgments

We thank Manju Siliwal for her invaluable contribution; Andrea Griffin for her guidance and helpful advice; Francoise Lermite for her support and help with statistical analysis; Shahar Zanzuri, Lior Davis and Daniel Yagoda for their help with data analysis; Ori Peleg for his help with study design; and Srinivas Yellapau for his help with molecular lab work. We thank the Israel Nature and Parks Authority (INPA) and Uttarakhand State Forest Department for providing permits. We particularly thank Dr Dhananjai Mohan, Dr V. B. Mathur and Dr G. S. Rawat for providing support in undertaking the study in India. We also thank the numerous individuals who helped capture and care for birds including Yotam Ghendler, Eyal Deri, Yonatan Veronski, Giselle Hazan, Doron Nissim, Ori Linial, Eran Hymes, Ohad Hatozfe, Mark Katz, Gal Bismuth, Mati Dinur, Ron Efrat, Yoav Motro, Sveta Weismann, Ron Elazari, Ehud Katzir, Hadar Yosifon, Darren Burns, Snir Halle, Yael Lehnardt, Gonen Bahir, Asaf Kaplan, Zehava Siegal, Amir Shafir, Hala Kasis, Imam Hussain, Mohammad Rafi, Deven Mehta, Hareendra Baraiya, Sarabjeet and Ankita Bhatt. We thank three anonymous referees and the editor, Mike Webster, for their thorough and constructive review. This work was supported by the Tel Aviv University Global Research & and Training Fellowship in Medical and Life Sciences (GRTF) fund, The Smaller-Winnikow Fellowship Fund for Environmental Research, The Rieger Foundation–Jewish National Fund fellowship, and the Heredity Fieldwork Grant of the Genetics Society U.K. This research was also supported by Grant No. 2017285 (to R.D. and M.E.H.) from The United States–Israel Binational Science Foundation (BSF). R.S.K. and M.N. received an inhouse grant from the Wildlife Institute of India for undertaking fieldwork in India.

References

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Price, T. D., & Ketterson, E. D. (2014). Hormonal, behavioral, and life-history traits exhibit correlated shifts in relation to population establishment in a novel environment. *American Naturalist, 184*(6), E147–E160.

Barton, K. (2018). *MuMIn: Multi-model inference*. R package version 1.40.4 https://CRAN.R-project.org/package=MuMIn.

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters, 12*(2), 24–27.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution, 24*(3), 127–135.

Candler, S., & Bernal, X. E. (2015). Differences in neophobia between cane toads from introduced and native populations. *Behavioral Ecology, 26*(1), 97–104.

Chapple, D. G., Simmonds, S. M., & Wong, B. B. M. (2012). Can behavioral and personality traits influence the success of unintentional species introductions? *Trends in Ecology & Evolution, 27*(1), 57–62.

Chaves, L. F. (2010). An entomologist guide to demystify pseudoreplication: Data analysis of field studies with design constraints. *Journal of Medical Entomology, 47*(3), 291–298.

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K., & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: Group composition matters. *Proceedings of the Royal Society B: Biological Sciences, 278*(1712), 1670–1678.

Cramp, S., & Perrins, C. M. (1994). *The birds of the western Palearctic vol VIII: crows to finches*. Oxford, U.K.: Oxford University Press.

Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences, 104*(38), 15017–15022.

Fridolfsson, A.-K., & Ellegren, H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology, 30*, 116–121.

Genovesi, P., & Shine, C. (2004). *European strategy on invasive alien species: Convention on the Conservation of European Wildlife and Habitats (Bern Convention) (Nature and Environment No. 137)*. Strasbourg, France: Council of Europe Publishing.

Greenberg, R., & Mettke-Hofmann, C. (2001). Ecological aspects of neophobia and neophilia in birds. *Current Ornithology, 16*, 119–178.

Greenberg, R., Reader, S. M., & Laland, K. N. (2003). The role of neophobia in the development of innovative behaviour of birds. In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 175–196). New York, NY: Oxford University Press.

Griffin, A. S. (2008). Socially acquired predator avoidance: Is it just classical conditioning? *Brain Research Bulletin, 76*(3), 264–271.

Griffin, A. S., & Boyce, H. M. (2009). Indian mynahs, *Acridotheres tristis*, learn about dangerous places by observing the fate of others. *Animal Behaviour, 78*(1), 79–84.

Griffin, A. S., & Diquelou, M. C. (2015). Innovative problem solving in birds: A cross-species comparison of two highly successful passerines. *Animal Behaviour, 100*, 84–94.

Griffin, A. S., Diquelou, M., & Perea, M. (2014). Innovative problem solving in birds: A key role of motor diversity. *Animal Behaviour, 92*, 221–227.

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes, 109*, 121–134.

Griffin, A. S., Guez, D., Lermite, F., & Patience, M. (2013a). Tracking changing environments: Innovators are fast, but not flexible learners. *PloS One, 8*(12). e84907.

Griffin, A. S., Lermite, F., Perea, M., & Guez, D. (2013b). To innovate or not: Contrasting effects of social groupings on safe and risky foraging in Indian mynahs. *Animal Behaviour, 86*(6), 1291–1300.

Griffin, A. S., Netto, K., & Peneaux, C. (2017). Neophilia, innovation and learning in an urbanized world: A critical evaluation of mixed findings. *Current Opinion in Behavioral Sciences, 16*, 15–22.

Gruber, J., Brown, G., Whiting, M. J., & Shine, R. (2017a). Geographic divergence in dispersal-related behaviour in cane toads from range-front versus range-core populations in Australia. *Behavioral Ecology and Sociobiology, 71*(2), 38.

Gruber, J., Brown, G., Whiting, M. J., & Shine, R. (2017b). Is the behavioural divergence between range-core and range-edge populations of cane toads (*Rhinella marina*) due to evolutionary change or developmental plasticity? *Royal Society Open Science, 4*(10), 170789.

Gruber, J., Brown, G., Whiting, M. J., & Shine, R. (2018). Behavioural divergence during biological invasions: A study of cane toads (*Rhinella marina*) from contrasting environments in hawai'i. *Royal Society Open Science, 5*(4), 180197.

Gruber, J., Whiting, M. J., Brown, G., & Shine, R. (2017). The loneliness of the long-distance toad: Invasion history and social attraction in cane toads (*Rhinella marina*). *Biology Letters, 13*(11), 20170445.

Gruber, J., Whiting, M. J., Brown, G., & Shine, R. (2018). Effects of rearing environment and population origin on responses to repeated behavioural trials in cane toads (*Rhinella marina*). *Behavioural Processes, 153*, 40–46.

Holzapfel, C., Levin, N., Hatzofe, O., & Kark, S. (2006). Colonisation of the Middle East by the invasive Common Myna *Acridotheres tristis L.*, with special reference to Israel. *Sandgrouse, 28*(1), 44.

Hubbard, L., King, W., Vu, A., & Blumstein, D. T. (2015). Heterospecific nonalarm vocalizations enhance risk assessment in common mynas. *Behavioral Ecology, 26*(2), 632–638.

Ingley, S. J., & Johnson, J. B. (2014). Animal personality as a driver of reproductive isolation. *Trends in Ecology & Evolution, 29*(7), 369–371.

Juette, T., Cucherousset, J., & Cote, J. (2014). Animal personality and the ecological impacts of freshwater non-native species. *Current Zoology, 60*(3), 417–427.

Kolar, C. S., & Lodge, D. M. (2001). Progress in invasion biology: Predicting invaders. *Ecology & Evolution, 16*(4), 199–204.

Lee, M. S. Y. (2011). Macroevolutionary consequences of “spatial sorting”. *Proceedings of the National Academy of Sciences, 108*(31). E347–E347.

Lermite, F., Peneaux, C., & Griffin, A. S. (2017). Personality and problem-solving in common mynas (Acridotheres tristis). *Behavioural Processes, 134*, 87–94.

Liebl, A. L., & Martin, L. B. (2012). Exploratory behaviour and stressor hyper responsiveness facilitate range expansion of an introduced songbird. *Proceedings of the Royal Society B: Biological Sciences, 279*(1746), 4375–4381.

Liebl, A. L., & Martin, L. B. (2014). Living on the edge: Range edge birds consume novel foods sooner than established ones. *Behavioral Ecology, 25*(5), 1089–1096.

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the world's worst invasive alien species: a selection from the global invasive species database* (Vol. 12). Auckland, New Zealand: Invasive Species Specialist Group Auckland.

Magory Cohen, T., & Dor, R. (2019). The effect of local species composition on the distribution of an avian invader. *Scientific Reports, 9*(1), 1–9.

Magory Cohen, T., McKinney, M., Kark, S., & Dor, R. (2019). Global invasion in progress: Modeling the past, current and potential global distribution of the common myna. *Biological Invasions, 21*(4), 1295–1309.

Martin, L. B., & Fitzgerald, L. (2005). A taste for novelty in invading house sparrows, *Passer domesticus*. *Behavioral Ecology, 16*(4), 702–707.

Mery, F., & Burns, J. G. (2010). Behavioural plasticity: An interaction between evolution and experience. *Evolutionary Ecology, 24*(3), 571–583.

Mevik, B.-H., & Wehrens, R. (2007). The pls package: Principal component and partial least squares regression in R. *Journal of Statistical Software, 18*(2), 1–23.

Mueller, J. C., Edelaar, P., Carrete, M., Serrano, D., Potti, J., Blas, J., et al. (2014). Behaviour-related DRD4 polymorphisms in invasive bird populations. *Molecular Ecology, 23*(11), 2876–2885.

Myles-Gonzalez, E., Burness, G., Yavno, S., Rooke, A., & Fox, M. G. (2015). To boldly go where no goby has gone before: Boldness, dispersal tendency, and metabolism at the invasion front. *Behavioral Ecology, 26*(4), 1083–1090.

Overington, S. E., Griffin, A. S., Sol, D., & Lefebvre, L. (2011). Are innovative species ecological generalists? A test in north American birds. *Behavioral Ecology, 22*(6), 1286–1293.

Pettit, L. J., Greenlees, M. J., & Shine, R. (2016). Is the enhanced dispersal rate seen at invasion fronts a behaviourally plastic response to encountering novel ecological conditions? *Biology Letters, 12*(9), 20160539.

Pintor, L. M., Sih, A., & Bauer, M. L. (2008). Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos, 117*(11), 1629–1636.

R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*(2), 291–318.

Rodriguez, L. F. (2006). Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions, 8*(4), 927–939.

Shine, R., Brown, G. P., & Phillips, B. L. (2011). An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences, 108*(14), 5708–5711.

Sol, D. (2003). Behavioural innovation: A neglected issue in the ecological and evolutionary literature? In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 63–82). New York, NY: Oxford University Press.

Sol, D., Griffin, A. S., & Bartomeus, I. (2012). Consumer and motor innovation in the common myna: The role of motivation and emotional responses. *Animal Behaviour, 83*(1), 179–188.

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PloS One, 6*(5). e19535.

Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour, 63*(3), 495–502.

Sol, D., Uncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, 102*(15), 5460–5465.

Suarez, A. V., Tsutsui, N. D., Holway, D. A., & Case, T. J. (1999). Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. *Biological Invasions, 1*(1), 43–53.

Suh, A., Kriegs, J. O., Brosius, J., & Schmitz, J. (2011). Retroposon insertions and the chronology of avian sex chromosome evolution. *Molecular Biology and Evolution, 28*(11), 2993–2997.

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*(1), 13–21.

Therneau, T. (2018). *Coxme: Mixed Effects Cox Models*. R Package Version 2.2-3, 2012. Retrieved from https://cran.r-project.org/package=coxme.

Tidemann, C. R., & Fenner School, A. N. U. (2009). *Common myna*. Retrieved from http://fennerschool-associated.anu.edu.au/myna/index.htm.

White, P. S., & Densmore, L. D. (1992). *Mitochondrial DNA isolation: Molecular genetic analysis of populations. A practical approach*. Oxford, U.K.: Oxford University Press.

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010). Behavioral flexibility and species invasions: The adaptive flexibility hypothesis. *Ethology Ecology & Evolution, 22*(4), 393–404.

Appendix

Table A1
Information on common mynas used in this study

Bird no.	Range	Locality	Country	Collection date	Age	Latitude	Longitude	Altitude (m)	Sex	Distance from source (km)	Years since invasion	Food composition
Atb 01	Nonfront	Nahariya	Israel	26 Sep 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 02	Nonfront	Nahariya	Israel	26 Sep 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 03	Nonfront	Nahariya	Israel	26 Sep 2016	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 04	Nonfront	Nahariya	Israel	26 Sep 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 05	Nonfront	Nahariya	Israel	4 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 06	Nonfront	Nahariya	Israel	4 Oct 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 07	Nonfront	Nahariya	Israel	4 Oct 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 08	Nonfront	Nahariya	Israel	4 Oct 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 09	Nonfront	Nahariya	Israel	11 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 10	Nonfront	Nahariya	Israel	11 Oct 2016	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 12	Nonfront	Nahariya	Israel	19 Oct 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 13	Nonfront	Nahariya	Israel	7 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 14	Nonfront	Nahariya	Israel	19 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 15	Nonfront	Nahariya	Israel	26 Oct 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 16	Nonfront	Nahariya	Israel	26 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 17	Nonfront	Nahariya	Israel	26 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 18	Nonfront	Nahariya	Israel	26 Oct 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 19	Nonfront	Nahariya	Israel	9 Nov 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 20	Nonfront	Nahariya	Israel	10 Nov 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 21	Nonfront	Nahariya	Israel	10 Nov 2016	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 22	Nonfront	Nahariya	Israel	10 Nov 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 23	Nonfront	Nahariya	Israel	16 Nov 2016	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 24	Nonfront	Nahariya	Israel	16 Nov 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 25	Nonfront	Nahariya	Israel	16 Nov 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 26	Nonfront	Nahariya	Israel	16 Nov 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 27	Nonfront	Nahariya	Israel	26 Nov 2016	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 28	Nonfront	Nahariya	Israel	26 Nov 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 29	Nonfront	Nahariya	Israel	26 Nov 2016	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 30	Nonfront	Nahariya	Israel	26 Nov 2016	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 31	Nonfront	Nahariya	Israel	1 Dec 2016	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 32	Nonfront	Nahariya	Israel	1 Dec 2016	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 33	Nonfront	Nahariya	Israel	1 Dec 2016	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 34	Front	Ma'on	Israel	8 Dec 2016	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 35	Front	Ma'on	Israel	8 Dec 2016	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 36	Front	Ma'on	Israel	8 Dec 2016	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 37	Front	Ma'on	Israel	8 Dec 2016	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 38	Front	Ma'on	Israel	16 Dec 2016	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 39	Front	Ma'on	Israel	16 Dec 2016	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 40	Nonfront	Tel Aviv	Israel	16 Dec 2016	Adult	32.11235	34.808357	37	M	0	20	Mixture 1
Atb 41	Nonfront	Tel Aviv	Israel	16 Dec 2016	Adult	32.11235	34.808357	37	F	0	20	Mixture 1
Atb 42	Front	Ma'on	Israel	25 Dec 2016	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 43	Front	Ma'on	Israel	25 Dec 2016	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 44	Front	Ma'on	Israel	15 Feb 2017	Juvenile	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 45	Front	Ma'on	Israel	15 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 46	Front	Ma'on	Israel	15 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 47	Front	Ma'on	Israel	15 Feb 2017	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 48	Front	Ma'on	Israel	20 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 49	Front	Ma'on	Israel	20 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 50	Front	Ma'on	Israel	20 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 51	Front	Ma'on	Israel	25 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 52	Front	Ma'on	Israel	25 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 53	Front	Ma'on	Israel	25 Feb 2017	Adult	31.414592	35.163893	784	M	83.12	2	Mixture 1
Atb 54	Front	Ein Afek	Israel	3 Mar 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 1
Atb 55	Front	Ein Afek	Israel	3 Mar 2017	Adult	32.84674	35.111746	15	F	87.6	1	Mixture 1
Atb 56	Nonfront	Tel Aviv	Israel	3 Mar 2017	Adult	32.11235	34.808357	37	F	0	20	Mixture 1
Atb 57	Front	Ein Afek	Israel	8 Mar 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 1
Atb 58	Nonfront	Tel Aviv	Israel	8 Mar 2017	Adult	32.11235	34.808357	37	F	0	20	Mixture 1
Atb 59	Front	Ein Afek	Israel	8 Mar 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 1
Atb 60	Front	Ma'on	Israel	18 Mar 2017	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 61	Nonfront	Tel Aviv	Israel	18 Mar 2017	Adult	32.11235	34.808357	37	M	0	20	Mixture 1
Atb 62	Nonfront	Tel Aviv	Israel	18 Mar 2017	Adult	32.11235	34.808357	37	F	0	20	Mixture 1
Atb 63	Front	Ein Afek	Israel	18 Mar 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 1
Atb 64	Front	Ein Afek	Israel	18 Mar 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 1
Atb 65	Front	Ein Afek	Israel	23 Mar 2017	Adult	32.84674	35.111746	15	F	87.6	1	Mixture 1
Atb 66	Nonfront	Mishmar Hayarden	Israel	28 Mar 2017	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 1
Atb 67	Nonfront	Mishmar Hayarden	Israel	28 Mar 2017	Adult	33.00348	35.598271	228	M	124.69	14	Mixture 1
Atb 68	Front	Ma'on	Israel	11 Apr 2017	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 69	Front	Ma'on	Israel	11 Apr 2017	Adult	31.414592	35.163893	784	F	83.12	2	Mixture 1
Atb 70	Nonfront	Tel Aviv	Israel	3 May 2017	Adult	32.11235	34.808357	37	M	0	20	Mixture 1
Atb 71	Nonfront	Tel Aviv	Israel	3 May 2017	Adult	32.11235	34.808357	37	M	0	20	Mixture 1

Table A1 (*continued*)

Bird no.	Range	Locality	Country	Collection date	Age	Latitude	Longitude	Altitude (m)	Sex	Distance from source (km)	Years since invasion	Food composition
Atb 72	Nonfront	Tel Aviv	Israel	15 May 2017	Adult	32.11235	34.808357	37	M	0	20	Mixture 1
Atb 73	Nonfront	Tel Aviv	Israel	20 May 2017	Adult	32.11235	34.808357	37	F	0	20	Mixture 1
Atb 74	Nonfront	Mishmar Hayarden	Israel	24 May 2017	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 1
Atb 75	Nonfront	Nahariya	Israel	16 Aug 2017	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 76	Nonfront	Nahariya	Israel	16 Aug 2017	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 77	Nonfront	Nahariya	Israel	16 Aug 2017	Juvenile	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 78	Nonfront	Nahariya	Israel	16 Aug 2017	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 1
Atb 79	Nonfront	Nahariya	Israel	16 Aug 2017	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 1
Atb 80	Nonfront	Nahariya	Israel	2 Nov 2017	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 81	Nonfront	Nahariya	Israel	2 Nov 2017	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 82	Nonfront	Nahariya	Israel	2 Nov 2017	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 83	Nonfront	Nahariya	Israel	2 Nov 2017	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 84	Nonfront	Nahariya	Israel	2 Nov 2017	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 2
Atb 85	Nonfront	Nahariya	Israel	9 Nov 2017	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 86	Nonfront	Nahariya	Israel	9 Nov 2017	Adult	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 87	Nonfront	Nahariya	Israel	9 Nov 2017	Juvenile	33.00854	35.098051	13	F	104.38	7	Mixture 2
Atb 88	Nonfront	Nahariya	Israel	9 Nov 2017	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 2
Atb 89	Nonfront	Nahariya	Israel	9 Nov 2017	Adult	33.00854	35.098051	13	M	104.38	7	Mixture 2
Atb 90	Front	Ein Afek	Israel	6 Dec 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 2
Atb 91	Front	Ein Afek	Israel	6 Dec 2017	Adult	32.84674	35.111746	15	F	87.6	1	Mixture 2
Atb 92	Front	Ein Afek	Israel	6 Dec 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 2
Atb 93	Nonfront	Tel Aviv	Israel	22 Dec 2017	Adult	32.11235	34.808357	37	M	0	20	Mixture 2
Atb 94	Front	Ein Afek	Israel	6 Dec 2017	Adult	32.84674	35.111746	15	M	87.6	1	Mixture 2
Atb 95	Nonfront	Tel Aviv	Israel	13 Jan 2018	Adult	32.11235	34.808357	37	M	0	20	Mixture 2
Atb 96	Nonfront	Tel Aviv	Israel	19 Jan 2018	Adult	32.11235	34.808357	37	F	0	20	Mixture 2
Atb 97	Nonfront	Tel Aviv	Israel	29 Jan 2018	Adult	32.11235	34.808357	37	F	0	20	Mixture 2
Atb 98	Front	Ein Afek	Israel	29 Jan 2018	Adult	32.84674	35.111746	15	F	87.6	1	Mixture 2
Atb 99	Nonfront	Mishmar Hayarden	Israel	29 Jan 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 100	Nonfront	Mishmar Hayarden	Israel	29 Jan 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 101	Nonfront	Mishmar Hayarden	Israel	7 Feb 2018	Adult	33.00348	35.598271	228	M	124.69	14	Mixture 2
Atb 102	Front	Kmehin	Israel	7 Feb 2018	Adult	30.91033	34.430725	220	F	138.02	1	Mixture 2
Atb 106	Nonfront	Mishmar Hayarden	Israel	14 Feb 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 107	Nonfront	Mishmar Hayarden	Israel	14 Feb 2018	Adult	33.00348	35.598271	228	M	124.69	14	Mixture 2
Atb 108	Nonfront	Tel Aviv	Israel	14 Feb 2018	Adult	32.11235	34.808357	37	M	0	20	Mixture 2
Atb 109	Nonfront	Mishmar Hayarden	Israel	14 Feb 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 110	Nonfront	Tel Aviv	Israel	21 Feb 2018	Adult	32.11235	34.808357	37	M	0	20	Mixture 2
Atb 111	Nonfront	Tel Aviv	Israel	21 Feb 2018	Adult	32.11235	34.808357	37	F	0	20	Mixture 2
Atb 112	Nonfront	Tel Aviv	Israel	21 Feb 2018	Adult	32.11235	34.808357	37	F	0	20	Mixture 2
Atb 113	Nonfront	Tel Aviv	Israel	21 Feb 2018	Adult	32.11235	34.808357	37	F	0	20	Mixture 2
Atb 114	Nonfront	Tel Aviv	Israel	28 Feb 2018	Adult	32.11235	34.808357	37	M	0	20	Mixture 2
Atb 115	Front	Sde Boker	Israel	28 Feb 2018	Adult	30.8523	34.7834	479	F	139.73	4	Mixture 2
Atb 116	Nonfront	Mishmar Hayarden	Israel	28 Feb 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 117	Front	Ein Afek	Israel	28 Feb 2018	Adult	32.84674	35.111746	15	F	87.6	1	Mixture 2
Atb 118	Front	Merom Golan	Israel	28 Feb 2018	Adult	33.13258	35.777071	987	F	145.14	1	Mixture 2
Atb 119	Nonfront	Mishmar Hayarden	Israel	14 Mar 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 120	Nonfront	Mishmar Hayarden	Israel	14 Mar 2018	Adult	33.00348	35.598271	228	M	124.69	14	Mixture 2
Atb 121	Nonfront	Mishmar Hayarden	Israel	14 Mar 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 122	Nonfront	Mishmar Hayarden	Israel	23 Mar 2018	Adult	33.00348	35.598271	228	F	124.69	14	Mixture 2
Atb 123	Nonfront	Mishmar Hayarden	Israel	23 Mar 2018	Adult	33.00348	35.598271	228	M	124.69	14	Mixture 2
B89010B	Native	Dehradun	India	6 Sep 2017	Juvenile	30.28077	77.971193	599	F	–	–	Mixture 3
B89021	Native	Dehradun	India	13 Sep 2017	Adult	30.2816	77.971913	600	F	–	–	Mixture 3
B89025	Native	Dehradun	India	16 Sep 2017	Adult	30.28569	77.965429	593	M	–	–	Mixture 3
B89026	Native	Dehradun	India	17 Sep 2017	Adult	30.28569	77.965429	593	F	–	–	Mixture 3
B89027	Native	Dehradun	India	17 Sep 2017	Adult	30.28569	77.965429	593	M	–	–	Mixture 3
B89031	Native	Haridwar	India	10 Dec 2017	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89033	Native	Haridwar	India	25 Dec 2017	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89033A	Native	Haridwar	India	31 Dec 2017	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89034	Native	Haridwar	India	25 Dec 2017	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89035	Native	Haridwar	India	27 Dec 2017	Adult	29.77227	78.255675	284	M	–	–	Mixture 3
B89036	Native	Haridwar	India	5 Jan 2018	Adult	29.77227	78.255675	284	M	–	–	Mixture 3
B89037	Native	Haridwar	India	7 Jan 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89038	Native	Haridwar	India	7 Jan 2018	Adult	29.77227	78.255675	284	M	–	–	Mixture 3
B89040	Native	Haridwar	India	16 Jan 2018	Adult	29.77227	78.255675	284	M	–	–	Mixture 3
B89041	Native	Haridwar	India	15 Jan 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89042	Native	Haridwar	India	22 Jan 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89043	Native	Haridwar	India	3 Jan 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89044	Native	Haridwar	India	11 Feb 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89045	Native	Haridwar	India	28 Feb 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89046	Native	Haridwar	India	2 Mar 2018	Adult	29.77227	78.255675	284	M	–	–	Mixture 3
B89047	Native	Haridwar	India	2 Mar 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89048	Native	Haridwar	India	9 Mar 2018	Adult	29.77227	78.255675	284	M	–	–	Mixture 3
B89049	Native	Haridwar	India	13 Mar 2018	Adult	29.77227	78.255675	284	F	–	–	Mixture 3
B89050	Native	Dehradun	India	20 Mar 2018	Adult	30.28569	77.965429	593	M	–	–	Mixture 3
B89051	Native	Dehradun	India	20 Mar 2018	Adult	30.28569	77.965429	593	F	–	–	Mixture 3

Localities correspond to locations displayed on the maps in Fig. 1. F: female; M: male.

Table A2
Percentage of individuals that succeeded in solving each of the behavioural tasks as a function of population type

Behavioural task	Percentage of successful individuals (total *N*)		
	Front	Nonfront	Native
Object neophobia	96.97 (33)	88.37 (43)	95.65 (23)
Food neophobia	91.43 (35)	87.50 (48)	52.17 (23)
Motor innovation (easy)	75.00 (28)	43.24 (37)	21.74 (23)
Motor innovation (difficult)	33.33 (24)	21.05 (38)	5.00 (20)

N is the total sample size of the task.

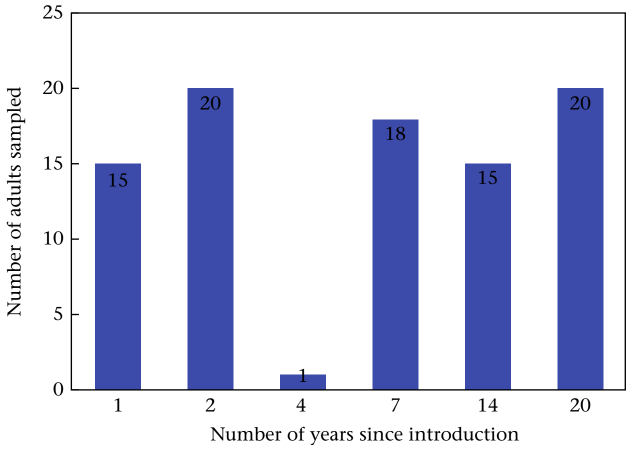

Figure A1. The number of adults sampled in the introduced population (Israel) as a function of the number of years since the arrival of the first invaders in the respective locality. Numbers in bars are numbers of adults sampled.