



Detrimental effects of urbanization on the diet, health, and signal coloration of an ecologically successful alien bird

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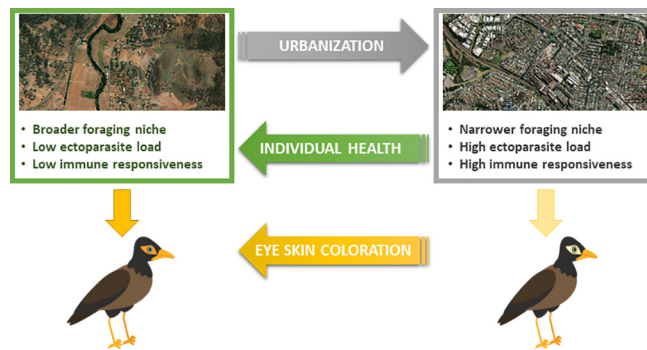
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HIGHLIGHTS

- Ecological conditions in overcrowded cities may lead to unhealthy condition for birds.
- High urbanization decreased the foraging niche of alien bird populations.
- Eye skin coloration and health status decreased in high urban environments.
- Resource competition and suboptimal conditions in cities may drive spread of aliens.

GRAPHICAL ABSTRACT



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ABSTRACT

Theory suggests that overcrowding and increased competition in urban environments might be detrimental to individual condition in avian populations. Unfavourable living conditions could be compounded by changes in dietary niche with additional consequences for individual quality of urban birds. We analysed the isotopic signatures, signal coloration, body condition, parasitic loads (feather mites and coccidia), and immune responsiveness of 191 adult common (Indian) mynas (*Acridotheres tristis*) captured in 19 localities with differing levels of urbanization. The isotopic signature of myna feathers differed across low and high urbanized habitats, with a reduced isotopic niche breadth found in highly urbanized birds. This suggests that birds in high urban environments may occupy a smaller foraging niche to the one of less urbanized birds. In addition, higher degrees of urbanization were associated with a decrease in carotenoid-based coloration, higher ectoparasite loads and higher immune responsiveness. This pattern of results suggests that the health status of mynas from more urbanized environments was poorer than mynas from less modified habitats. Our findings are consistent with the theory that large proportions of individual birds that would otherwise die under natural conditions survive due to prevailing top-down and bottom-up ecological processes in cities. Detrimental urban ecological conditions and search for more favourable, less crowded habitats offers the first reasonable explanation for why an ecological invader like the common myna continues to spread within its global invasive range.

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1. Introduction

Urbanization is the fastest form of anthropogenic transformation of natural ecosystems (Angel et al., 2011). Increase in human-made structures are associated with a very significant restructuring of plant and animal communities (McKinney, 2002, 2008; Seto et al., 2012; Shanahan et al., 2013), high pollution levels (Grimm et al., 2008; Murray et al., 2016; Shanahan et al., 2013) and an increase of pathogen and disease transmissions among wildlife (Bradley and Altizer, 2007; Jones and James Reynolds, 2008; Murray et al., 2016). These ecological perturbations and their effects have been studied extensively in birds (Aronson et al., 2014; Evans, 2010; Shochat, 2004). In cities, avian species richness is reduced drastically relative to natural habitats, despite a significant increase in biomass dominated by a few native but more often, alien species (Grarock et al., 2014; Kark et al., 2007; Marzluff, 2001; Møller et al., 2012; Shochat et al., 2010b).

There have been attempts to model and quantify the ecological processes that underpin these now well described patterns of avian species loss and density increase typical of cities (Marzluff et al., 2001; Møller et al., 2012; Shochat et al., 2010b; Sol et al., 2012). For example, Shochat (2004) proposed that high avian population densities are attributable to high abundance and predictability of food sources (bottom-up processes) combined with a reduced predation risk (top-down processes). High densities produce overcrowding, however, which in turn increases parasite transmission (Bradley et al., 2008; Delgado-V and French, 2015; Sykes et al., 2020) and competition for resources (Shochat, 2004). Empirical and theoretical research suggest that only the best competitors and the most efficient foragers secure enough resources to reproduce (Shochat, 2004; Shochat et al., 2004). According to Shochat's (2004) theory, a large proportion of an urban avian population lives in poor body condition, but survives thanks to low predation and predictable food resources, contributing to large population sizes typical of cities (Marzluff, 2001; Møller et al., 2012).

The effect of competition on individual condition in overcrowded cities might well be exacerbated by poor resource quality. Although anthropogenic food sources (e.g. human discards, pet foods, bird feeders) are suggested to be more abundant and predictable in cities, their nutritional composition often differs from that of natural foods (Coogan et al., 2017, 2018; Pierotti and Annett, 1987). It has been suggested that abundant urban food sources can be inadequate in terms of allowing individuals to meet their nutritional and physiological needs (Heiss et al., 2009; Liker et al., 2008; Pierotti and Annett, 2001; Pollock et al., 2017; Schoech and Bowman, 2001). For example, studies in birds indicate that nestlings from urban and suburban areas can be nutrient restricted due to being fed unsuitable foods, which could ultimately lead to lower reproductive success in urban populations (Heiss et al., 2009; Pollock et al., 2017). Moreover, high quality natural food sources in the form of insects and other invertebrates are likely to be less abundant due to the loss of natural vegetation during the urbanization process (Heiss et al., 2009; Helden et al., 2012; Meyrier et al., 2017; Rickman and Connor, 2003; Sánchez-Bayo and Wyckhuys, 2019). Additional evidence for impoverished food resources in cities has arisen from studies of carotenoid colouration in bird. The production of carotenoid-based morphological signals are dependent upon nutrition and individual condition (Biard et al., 2017; Hill, 2000; Saks et al., 2003; Sumasgutner et al., 2018). There is a general agreement that carotenoid-based coloration decrease in urban environments, and is likely related to the lack of high-quality, natural, food sources (Hörak et al., 2000; Isaksson, 2009; Isaksson and Andersson, 2007; for a review see, Peneaux et al., 2021a). As a result, a reduction in the availability of natural foods could generate an increased in competition for rare, high-quality foods and accentuate the differences in individual quality between the few individuals able to monopolize them and those who cannot (Shochat, 2004). Research comparing birds from urban versus natural/rural habitats along multiple dimensions has shown that urban birds occupy a different dietary niche, consume poor quality foods, and tend to be

unhealthy and less coloured (Audet et al., 2016; Bradley and Altizer, 2007; Isaksson and Andersson, 2007; Murray et al., 2018; Peneaux et al., 2021a; Pollock et al., 2017; Seress et al., 2012).

Whether or not urban populations are mostly in poor condition and unable to reproduce is particularly important for understanding and predicting the spread of alien birds. Although alien species often constitute the majority of occupants in cities (Grarock et al., 2014; Marzluff, 2001; Møller et al., 2012; Shochat et al., 2010b), we do not know whether detrimental living conditions in overcrowded cities are the driver of range-expansion for those species that are invasive. Aliens could initially thrive in urban environments as a result of overabundant unexploited resources (ecological opportunism; Sol et al., 2012), low competition from the local community and low predation pressure. Once ecological conditions become detrimental to reproduction, however, increasingly competitive, deteriorating living conditions could favour range-expanding phenotypes and drive species spread. Such phenotypical shifts in response to resource competition and shortage have been found in Western bluebirds (*Sialia mexicana*) (Aguillon and Duckworth, 2015; Duckworth, 2009) and European starlings (*Sturnus vulgaris*) (Hui et al., 2012). Although range-expanding phenotypes might maintain their patterns of urban association and spatial segregation from native communities by island-hopping from one urban centre to another, they might also shift to occupying more natural habitat types where natives are more prevalent. Understanding the risk of such transitions can help target population control in space and time (Diquelou and Griffin, 2020; Rogers et al., 2020).

The invasive common (Indian) myna (*Acridotheres tristis*; hereafter myna) is an ideal model to investigate the costs of urban living, their potential to drive range expansion, and the ensuing risk of increased competition with native birds. The species is a highly commensal passerine native to India and south-east Asia (Feare and Craig, 1998), which is present and continues to spread in several countries across the globe (Ewart et al., 2019; Forsys and Allen, 1999; Holzapfel et al., 2006; IUCN Global Invasive Species Database, 2021; Khoury et al., 2021; Magory Cohen et al., 2019). This species is one of only three birds to be nominated by the Invasive Species Specialist Group as the "100 World's Worst" invaders (Lowe et al., 2000). Consistent with alien birds worldwide, myna population density rises along a gradient of increasing urban cover (i.e. impervious, sealed surfaces such as concrete and asphalt) and can reach very high abundances under conditions of high impervious cover (Dyer et al., 2017a, 2017b; Grarock et al., 2014; Handal and Qumsiyeh, 2021; Haythorpe et al., 2014; Khoury et al., 2021; Lazarina et al., 2020; Magory Cohen et al., 2019; Old et al., 2014; Sol et al., 2012). Mynas feed frequently on anthropogenic food sources and are found most often using artificial structures to nest (Khoury et al., 2021; Lowe et al., 2011; Machovsky-Capuska et al., 2016; Sengupta, 1976; Sol et al., 2012). These patterns of habitat selectivity, which are found consistently across the myna's global invasive range (Grarock et al., 2014; Khoury et al., 2021; Magory Cohen et al., 2019; Old et al., 2014; Peacock et al., 2007), are often considered evidence that mynas prefer urban habitat and therefore pose little risk to native species due to spatial segregation (Shochat et al., 2010a; Sol et al., 2013, 2014). There is convergent evidence, however, that the diet of mynas in urban habitats might be nutritionally deficient. When given the choice between foods with different nutritional content, urban mynas have been showed to selectively consume and fight for foods enriched in protein (Machovsky-Capuska et al., 2016). A follow-up study demonstrated that mynas kept on a low protein diet in captivity subsequently prioritised intake of foods with a high protein content (Peneaux et al., 2017). Further work has also shown that captive mynas on a low-lipid diet would prioritise intake in lipids (Gumede and Downs, 2020). This pattern of food selection and high levels of intraspecific aggression around specific nutrients strongly suggest that mynas might be experiencing nutritional limitations in urban habitats which contribute to increased competition, in consistency with Shochat's (2004) model. We argue that although mynas show a pattern

of selective association with urban habitats in their invasive range, these conditions might exclude many individuals from reproducing as predicted by Shochat (2004). Reduced access to essential food sources, particularly those important to breeding, might favour individuals that move to less densely occupied areas. These might be reached by island-hopping to yet unoccupied urban centres, thus avoiding overlap with native communities. But essential resources might also be reached by spreading to more natural habitats including urban parks and natural bushland at the edges of cities, with the added benefit of avoiding the energetic costs and risks of long-distance travel. Any transition to occupying such habitats would increase the likelihood of competitive interactions with native species and are therefore important to consider (Diquelou and Griffin, 2020).

Here, we investigate the extent to which urban ecological conditions create sub-optimal environments for breeding, thus possibly generating a driver for ongoing range expansion of mynas in Australia, but likely also in other areas of its invasive range (e.g. South Africa, Israel, USA). We sampled populations of mynas located in habitats with differential level of urbanization across New South Wales (NSW, Australia). We used stable isotope analysis (SIA) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) to infer dietary niche variation across urbanization levels. Consumer stable isotope ratios are integrated from their foods through time and thus trace foraging information (e.g. diet, habitat use), with $\delta^{13}\text{C}$ varying predominantly based on food web primary production (e.g. C3, C4, CAM photosynthesis) and $\delta^{15}\text{N}$ varying mostly with trophic level (due to fractionation and depletion of ^{14}N across trophic levels) (Inger and Bearhop, 2008; Post, 2002). Consequently, isotopic niches are widely used as proxies for dietary niche breadth (Jackson et al., 2011; Newsome et al., 2007; although see caveats in Shipley and Matich, 2020).

We also measured body condition, external and internal parasitic loads, and immune responsiveness of each myna. To these measures of condition, we added skin coloration because carotenoid-based displays are robust honest signals of individual quality in birds (Svensson and Wong, 2011; Weaver et al., 2018). Together, these parameters provided an integrated measure of individual quality, which we refer to as 'health', consistent with previous research in this area on which to assess the impact of urbanization (Murray et al., 2016, 2019; Sumasgutner et al., 2018). We predicted that isotopic niches (as proxies for dietary niches) would vary between areas of high and low urbanization. We also predicted that if mynas are affected by urban living conditions with high population densities, the health of common mynas should be reduced in more urbanized areas compared to less modified habitats.

2. Methods

2.1. Trapping sites and methods

A total of 191 adult mynas were trapped using walk-in baited traps (Tidemann, 2009) at 19 distinct sites within NSW (Australia) during non-breeding season between May and September of 2017 to 2020 (Fig. A.1). Mean distance between sample sites was 149.9 km, with distances ranging from 0.7 to 299.0 km. Each field site varied in the extent of sealed ground cover (Table 1). To provide a quantitative estimate of sealed ground cover at each of site, the GPS coordinates of each trap were recorded and mapped using QGIS v3.10.2 (QGIS.org 2020). Following an adjusted methodology from Giraudeau and McGraw (2014), landsat-7 satellite images were downloaded from the U.S. Geological Survey website for the time periods during which trapping occurred at each traps and habitat was digitized by hand to identify total build-up, impervious, cover (e.g. asphalt, concrete) within a 500 m radius of each trap. This distance was based on the relatively small home range size (0.1 km²) and short travel distances reported in urban mynas (Berthouly-Salazar et al., 2012; Burstal et al., 2020; Kang, 1989, 1992). The total build-up cover within the 500 m radius was converted into a percentage and was used as an urbanization score for each trap.

Upon capture, birds were transported to the Central Animal House at the University of Newcastle, Callaghan campus. To limit potential parasitic transmissions during trapping and transport, birds were collected from individual traps within 6 h (up to 48 h if only a single bird was present within the trap) and were kept isolated from birds trapped at a different location during transport (e.g. by only transporting birds from one trap at a time or by using individual cages covered with blankets). We collected standard body measurements, and calculated body condition as the residuals saved from a linear regression between body mass (± 0.01 g) and tarsal bone length (± 0.01 mm) (Schulte-Hostedde et al., 2005). We also collected the first two primary feathers from the left wing to examine diet niche via SIA (Inger and Bearhop, 2008). Mynas were housed overnight in individual cages and all measurements were within 24 h after arrival to the research facilities. All measurements and samples could not be obtained from each individual, thus we reported sample sizes associated with all statistical tests.

Mynas are classified as an introduced pest species in Australia and are the target of ongoing pest management strategies. Thus, it is illegal to release mynas and all captured birds were euthanized after samples were collected (Griffin and Boyce, 2009). Sex was determined by post-mortem examination of reproductive organs.

Table 1
Data gathered on the 19 distinct sites sampled in NSW, Australia.

Capture site	Major city	GPS coordinates (latitude, longitude)	Sampling dates	Sample size	Habitat (% urban cover)
Mayfield industrial	Newcastle	−32.895216, 151.729639	21/07/18, 03/07/19	8	98.85
Bathurst downtown	Bathurst	−33.424534, 149.580108	08/07/20 to 28/07/20	2	97.07
Collaroy Plateau suburban	Sydney	−33.730778, 151.293242	23/05/2017	3	90.84
North Curl Curl beachside	Sydney	−33.762187, 151.296188	29/05/2017	2	87.15
Mayfield suburban	Newcastle	−33.439816, 151.735950	26/05/19 to 23/06/19	15	86.19
Kotara suburban	Newcastle	−32.948517, 151.691373	19/08/19 to 23/09/19	18	82.95
Blackbutt suburban	Newcastle	−32.933907, 151.707098	03/07/19 to 07/07/19	9	75.19
Warriewood beachside	Sydney	−33.693174, 151.305846	29/05/2017	4	61.70
Bathurst suburban	Bathurst	−33.413706, 149.558556	25/06/2020	4	59.16
East Tamworth urban	Tamworth	−31.098857, 150.938579	23/05/2017	3	58.78
Warriewood suburban	Sydney	−33.691950, 151.29113	29/05/2017	3	55.47
Westdale suburban	Tamworth	−31.089823, 150.874425	12/06/19 to 11/07/19	12	50.38
Greta downtown	Greta	−32.675122, 151.388800	08/07/19 to 09/07/19	12	43.77
Greta suburban	Greta	−32.669080, 151.386642	24/05/19 to 29/05/19	21	40.71
Bathurst edge	Bathurst	−33.439816, 149.579663	25/06/20 to 08/07/20	3	33.31
Krumbach downtown	Krumbach	−32.051899, 152.259202	9/06/2017	5	5.34
Nemingha rural	Tamworth	−31.112426, 151.003433	2/06/2017	8	3.94
Oswald rural	Greta	−32.701943, 151.421790	1/07/2019	6	3.56

2.2. Preparation of feather samples and SIA

We washed all feathers in a 2:1 chloroform:methanol solution to remove excess dirt and oils before drying them at 60 °C for 48 h (Reese et al., 2018; Reynolds et al., 2019; Tollington et al., 2019). Small fragments of feather vane were cut from the distal end and weighted into tin capsules (1–2 mg) for SIA ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Stable isotope values were determined with a Europa EA GSL Elemental analyser (Europa Scientific Inc., Cincinnati OH) coupled to a Hydra 20–22 automated Isoprime isotope ratio mass spectrometer (Sercon Ltd.; www.serconlimited.com) at the Griffith University Stable Isotope Laboratory in Brisbane, Queensland, Australia. Ten standards were run with each tray, which were Pee Dee belemnite (for $\delta^{13}\text{C}$) and atmospheric nitrogen (for $\delta^{15}\text{N}$). The SD for measurements of standards was 0–0.2‰ for $\delta^{13}\text{C}$ and 0–0.1‰ for $\delta^{15}\text{N}$.

Moult of the primary feathers in mynas is likely to begin towards the end of the breeding season (March–May) (Feare, 2015). Thus, by sampling in winter, a large majority of the birds (breeding adults and young adults) captured have recently moulted. Hence, the dietary pattern measured in this winter study are most likely relatively short-term (up to 3–4 months).

2.3. Coloration measurements

Reflectance curves of the eye patch, beak, and tarsus of mynas were collected over the wavelength range 300–700 nm (1520 reflectance data points) using an AvaSpec 2048 spectrophotometer and an AVALIGHT-XE light source (Avantes, Netherlands). The spectrometer set parameters were as follows: integration time, 50 ms; scan to average, 5 scans; strobe, 2 flashes per scan; and smoothing, 1 pixel. The reflectance sensor was calibrated for every bird with a WS-2 white reflectance standard and a black reference tile. AvaSoft software was used to record and standardize the measurements. Measurements of reflectance standards and birds were taken with a shielded, black anodised, aluminium probe cut at a 45° angle at the tip to avoid specular reflectance (Enderler, 1990; Stein and Uy, 2006). Three points were measured by placing the shielded probe on the outer edge, middle and inner edge of the left side eye patch, beak, and tarsus.

We analysed all measurements using a custom-made MATLAB program (available in Mendeley Data), calibrated for the U-type eyes of mynas (Enderler and Mielke, 2005). We estimated cone activation (ultraviolet-sensitive cone -UVS-), hue (angle in the two-dimensional LSMU colour space), chroma (the distance from the achromatic point in the tetrahedron) and luminance (the capture of the double cones) following established methods and calculations (Enderler et al., 2005; Enderler and Mielke, 2005). Repeatability for each colour variable was high ($r > 0.93$, $P < 0.001$), thus we used average values for each bird for the four colour variables.

2.4. Quantification of ecto- and endoparasitism

Mynas were individually housed in small cages for 24 h with ad libitum access to food and water. In the morning (between 07.00 and 08.00 am), we scraped fresh faecal samples (ca. 0.5 g) from the cage into 1.5 ml screw-cap microcentrifuge tubes. Samples were stored in a fridge at 4 °C until analysis (1–2 days later). Using a faecal-float and slide preparation method (Giraudeau et al., 2014), we measured the presence and severity of coccidian infection (*Isospora* sp.) with a light microscope. Each slide was attributed a score based on the estimated number of oocyst present on the slide (presence of no oocysts = 1 - no infection, 1–1000 oocysts = 2 - moderate infection, >1000 oocysts = 3 - severe infection).

External level of parasites was assessed by estimating the number of feather mites attached to the primary and secondary feathers of the extended right wing exposed to a lamp (Harper, 1999). A score was established as a function of mites' abundancy on primary and secondary

feathers of the wing. The abundancy was scored as 1 = no mites, 2 = low presence of mites on primary or secondary only or low presence on both primary and secondary or high presence only on one type of feathers, and 3 = low presence on one type and high presence on the other or high presence on both primary and secondary.

2.5. Immune responsiveness assessment

To measure cellular immune responsiveness, a subcutaneous injection of phytohemagglutinin (PHA) was administered to mynas upon capture (Adelman et al., 2014; Bílková et al., 2015; Smits et al., 1999). Following Smits et al. (Smits et al., 1999) for similar sized birds, a dose of 0.05 mg of PHA (product no. L8754, Sigma-Aldrich, St Louis, MO, USA) dissolved in 0.05 ml of sterile PBS was delivered in the centre of the wing web (patagium). PHA induces a pro-inflammatory immune response that results in perivascular accumulation of various leukocytes and thickening of the skin that can be measured as a swelling. As a result, the thickness of the patagium was measured before injection and 24 h after injection with a micrometre calliper to the nearest 0.01 mm. We calculated the PHA-induced swelling response index as the difference between the tissue thickness 22.5 ± 1 h after injection minus the thickness before the PHA injection (Adelman et al., 2014; Bílková et al., 2015; Smits et al., 1999).

2.6. Statistical analyses

All statistical analyses were performed in R (v4.0.3; R Core Team, 2020) with an α value set to 0.05, except principal component analyses which were undertaken using JMP Pro (v14.2.0, SAS Institute Inc., Cary, NC; 2018).

To determine whether the foraging niche of mynas varied as a function of urbanization, we used feather stable isotope data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) obtained from 50 males and 50 females across 12 localities. First, we confirmed that sample C:N molar ratios were within acceptable ranges (mean \pm SD C:N = 3.24 ± 0.07 , range = 3.05–3.37) indicative of a protein substrate (C:N < 3.5; Post et al., 2007). To determine whether sex or urbanization influenced the isotopic niches of birds, bivariate standard ellipse areas (SEA) were fitted to their isotopic signatures using the SIBER package in R (Jackson et al., 2011). Male and female mynas were first assigned to either a low (urbanization score <75%; $n = 31$ males, 27 females) or high urbanization (urbanization score >75%; $n = 19$ males, 23 females) group based on the urbanization score of the location where they were captured. Subsequently small-sample corrected SEA (SEA_c), regions predicted to contain ~40% of observations and representing the core isotopic niche of each group (Jackson et al., 2011; Syväranta et al., 2013), were calculated for each sex and urbanization level. Bayesian SEA (SEA_b) were then estimated for these groups using Markov Chain Monte Carlo simulations (10,000 iterations, burn-in = 2000, thinning = 20, 2 chains), producing posterior distributions of 10,000 SEA_b estimates for each group which were then compared probabilistically to evaluate pairwise differences in isotopic niche breadth (Jackson et al., 2011). For two groups, i and j , pairwise comparisons were the proportion of posterior SEA_b estimates where $i < j$, which provides a proxy for the probability that these groups' posterior distributions differ scaling from 0 (low probability $i < j$, high probability $i > j$) to 1 (high probability $i < j$, low probability $i > j$), with values closer to 0.5 indicating greater similarity (Jackson et al., 2011). Differences were subsequently inferred where this probability was <0.05 ($i > j$) or >0.95 ($i < j$).

In addition to niche breadth, overlap was also estimated using the NicheROVER package (Swanson et al., 2015). For the purposes of overlap calculations, niche regions were computed from the posterior covariance matrix estimates output from SIBER Bayesian modelling, scaled as 95% prediction ellipses (Shipley et al., 2018; Swanson et al., 2015). Subsequently, overlap was determined following Swanson et al. (2015) and is interpreted as the probability that any randomly

drawn individual from group i falls within the 95% prediction ellipse of group j , which is directional because the overlap of i on j may differ from that of j on i . This was repeated for all posterior covariance matrix estimates for each group, producing posterior distributions for niche overlap between groups. These were compared probabilistically, as above, to determine whether overlaps between sexes and urbanization levels were directional (i.e. overlap i on $j \neq$ overlap j on i).

To determine whether signal coloration varied as a function of percent urbanization, we fitted a linear mixed effect model (LMMs; R package *lme4*; Bates et al., 2019). First, principal component analysis (PCA) was applied to the colour parameters (UVS, hue, chroma, luminance) in order to obtain a single colour score (Figuerola and Senar, 2005; Germain et al., 2010; MacDougall and Montgomerie, 2003; Quesada and Senar, 2007). From the coloration PCA, we extracted two principal component (PCs), which explained 89.6% of the variance. Hue (component loading >89%) and chroma (component loading >90%) loaded positively onto PC1 and UV (component loading >98%) loaded negatively. Brightness only positively loaded on PC2 (component loading >98%). PC1 scores were consistent with previous observations of colour variation within the eye patch of common mynas (Peneaux et al., 2020), where highly pigmented displays had redder hue, lowest UV signal and highest chroma and poorly pigmented displays had more yellow hue, highest UV signal and lowest chroma. As PC2 scores provided a measure of average reflectance but not pigmentation, they were not further analysed and PC1 scores were retained as carotenoid coloration scores. PC1 scores were then used as dependent variables for coloration in model. We included percent urbanization, sex, ornament type (eye patch, beak, tarsus) and their interactions as fixed effect predictors, with capture month and body condition as covariates. Trap ID and individual ID were entered as random effects in the model.

To determine whether myna's immune responsiveness varied as a function of percent urbanization, we modelled variation in PHA scores using LMMs. Percent urbanization, sex, and their interaction were included as predictor variables in the model. Capture month and body condition were also included as covariate and trap ID as a random effect. A similar linear model was fitted to test whether body condition varied as a function of percent urbanization. We used ordinal logistic regressions (*MASS* package; Venables and Ripley, 2002) to test whether parasite loads varied as a function of percent urbanization. We used

urbanization, sex, and the urbanization by sex interaction as predictors, body condition as covariate and coccidia score/mite score as the response. Capture month and trap ID were also initially included, but the models failed to converge.

3. Results

3.1. Variation in foraging niche

Mynas from more urban habitats had a significantly smaller niche ($SEA_c = 2.72$) than mynas from less urban habitats ($SEA_c = 5.71$, Table A.1B, Fig. 1A, B). Overlap between urbanization levels was also directional, with the overlap of high on low urbanization birds being greater than the overlap of low on high urbanization birds (Table A.2B), suggesting that high urbanization birds occupied a reduced subset of the low urbanization niche (Fig. 1A). The SEA_c was also slightly higher in females ($SEA_c = 4.97$) than in males ($SEA_c = 4.13$), although Bayesian modelling suggested no significant differences between sexes (Table A.1A). Likewise, the overlap of females on the male isotopic niche was high, and similar to that of males on females suggesting no directionality in overlaps among sexes (Table A.2A).

3.2. Variation in individual quality and health condition

3.2.1. Carotenoid-based coloration

The interaction of urbanization level and ornament type affected carotenoid coloration scores significantly (LMM, $F_{2, 208} = 11.63$, $p < 0.0001$, $N = 108$ individuals across 11 sites; Fig. 2A). Eye patch coloration was negatively related to urbanization level (LMM, $\beta = -0.027 \pm 0.009$, $t_{22} = -2.81$, $p = 0.01$), with individuals in less urbanized areas displaying more coloured eye patches. However, beak (LMM, $\beta = -0.006 \pm 0.009$, $t_7 = -0.65$, $p = 0.538$) and tarsus coloration (LMM, $\beta = -0.007 \pm 0.008$, $t_{10} = -0.79$, $p = 0.447$) did not differ with urbanization level (Fig. 2A).

In addition, individuals with higher eye patch coloration scores were also in better body condition (LMM, $\beta = 0.092 \pm 0.022$, $t_{102} = 4.13$, $p < 0.0001$; Fig. 2B) but beak and tarsus coloration scores were unrelated to body condition (LMMs, beak: $\beta = 0.013 \pm 0.015$, $t_{96} = 0.86$, $p =$

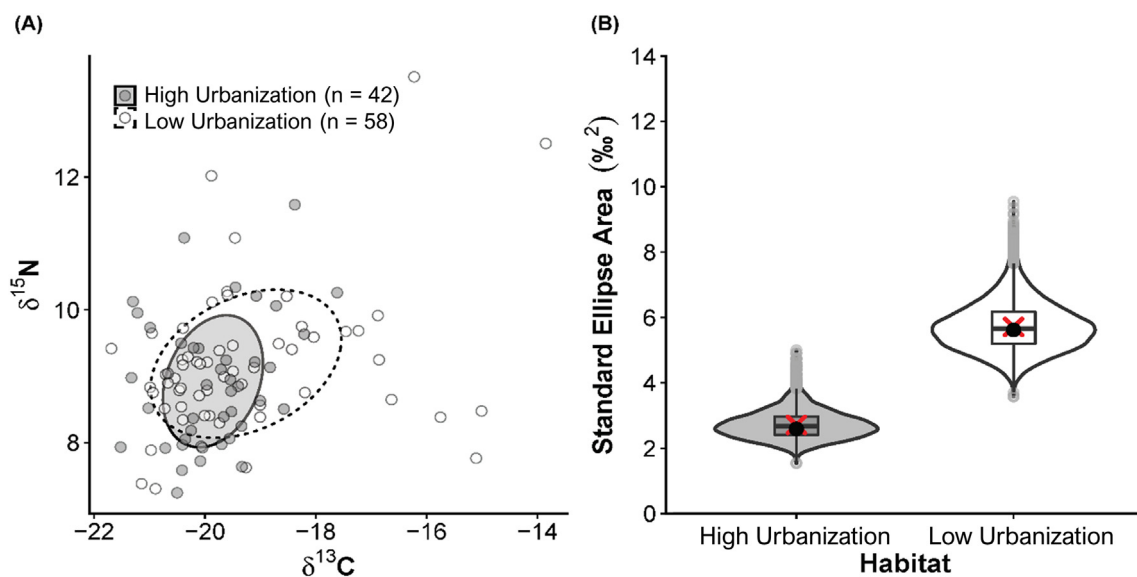


Fig. 1. Carbon and nitrogen stable isotope signatures (A) indicative of diet (basal food web source and trophic level, respectively) and small-sample corrected standard ellipse areas (SEA_c) as a measure of the foraging niche breadth of common mynas from areas of high and low urbanization. (B) Violin plots (box plots combined with a scaled kernel density trace) comparing the posterior distributions of Bayesian estimated standard ellipse areas ($SEAb$) between urbanization levels. Red crosses and black dots on the violin plots indicate maximum-likelihood estimated SEA_c (area of ellipses shown in (A)) and the mode of $SEAb$, respectively.

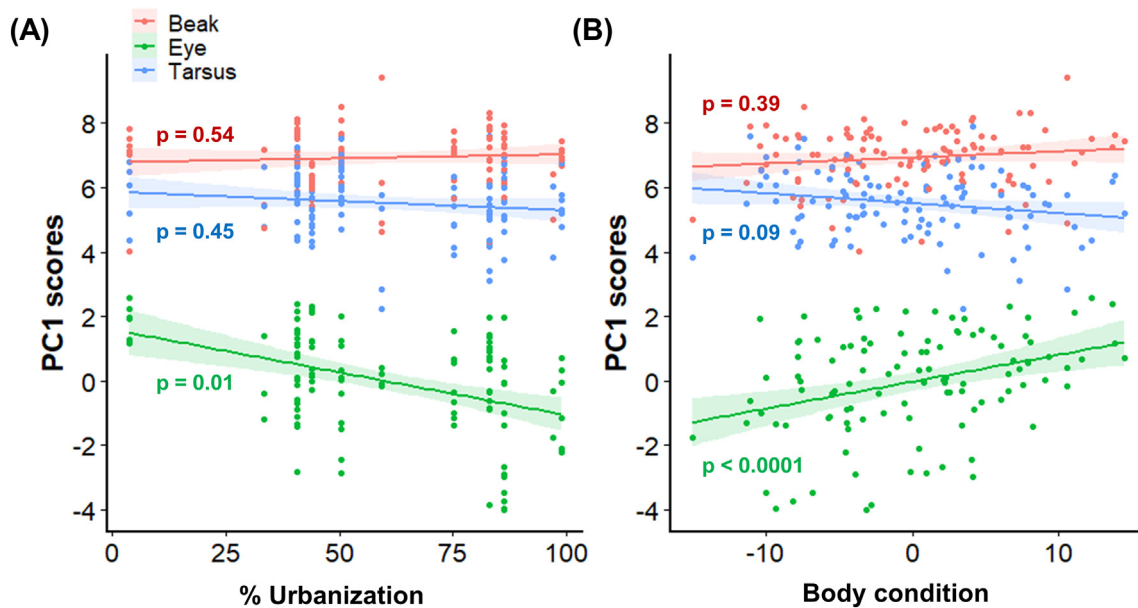


Fig. 2. Effect of % urbanization (A) and body condition (B) on the coloration of the beak (red), eye patch skin (green), and tarsus (blue) of common mynas. Model fit, 95% confidence intervals and p-values are shown for each body part.

0.392; tarsus: $\beta = -0.029 \pm 0.017$, $t_{99} = -1.73$, $p = 0.087$). Sex (LMM, $F_{1, 305} = 0.31$, $p = 0.575$) and capture month (LMM, $F_{4, 12} = 0.81$, $p = 0.541$) had no effect on coloration scores.

3.2.2. Endo- and ectoparasitic loads

The prevalence and severity of infection by ectoparasite was influenced by urbanization level (Table 2, Fig. 3A). Mynas living in low urban areas were more likely to show no sign of infection by feather mites (45.4%), while living in more urbanized areas increased the probability of moderate (27.7%) to high (17.7%) feather mite infestation. Body condition and sex had no effect on ectoparasitic infection (Table 2). In contrast, the severity of coccidial infection was not influenced by urbanization level and sex (Table 2). However, there was a significant effect of body condition on the severity of coccidial infection. Birds with higher body condition scores were less likely (44.6%) to have high coccidial loads (Table 2, Fig. 3B).

3.2.3. Immune responsiveness

Immune responsiveness, assessed via PHA-induced skin swelling, was positively related to urbanization level (LMM, $\beta = 0.002 \pm 0.001$, $t_{17} = 2.82$, $p = 0.012$, $N = 88$ individuals across 12 sites; Fig. 4A), such that birds sampled in more urbanized areas expressed stronger skin swelling. Sex (LMM, $F_{1, 75} = 0.10$, $p = 0.751$), body condition (LMM, $\beta = -0.001 \pm 0.002$, $t_{70} = -0.52$, $p = 0.608$) and capture month (LMM, $F_{3, 6} = 1.02$, $p = 0.449$) had no effect on PHA response.

3.2.4. Body condition

Body condition did not differ with urbanization level ($\beta = 0.036 \pm 0.037$, $t_{26} = 0.95$, $p = 0.350$, $N = 138$ individuals across 19 sites, Fig. 4B). Males were in better condition than females ($\beta = 5.098 \pm 2.292$, $t_{119} = 2.22$, $p = 0.028$). Month of capture was unrelated to body condition ($F_{4, 26} = 0.06$, $p = 0.993$).

4. Discussion

Understanding the proximate mechanisms of dispersion is key to predicting invasive species range expansions and planning management measures. This study aimed to determine whether common mynas, one of the most invasive birds globally, experience urban living conditions that might be driving the species' invasive dispersion along the East coast of Australia. We first compared the isotopic niche occupied by mynas captured in areas of high and low levels of urbanization. We also measured signal coloration as a proxy for individual and diet quality and adopted an integrative approach to estimate health condition in habitats with differential levels of urbanization. As predicted, the isotopic niche breadth differed significantly between mynas living in low and high urbanized environments, indicating disparities in their foraging strategies. We also found that birds were significantly less coloured at higher levels of urbanization, while immune responsiveness and ectoparasite loads were greater. We argue that urban living carries significant costs for mynas, possibly related to poor nutrition, which may in turn promote movements to environments where competition for, and access to, essential resources is lower.

Table 2

Ordinal logistic regression testing the effects of body condition, urbanization, sex, and their interaction on coccidia score and feather mite score. Metrics reported are mean and 95% credible intervals, likelihood ratio, degrees of freedom ("df") and p-values. Significant predictors of the corresponding response variable are in bold.

Dependent variables	N (ind, trap)	Factors	Mean (95% credible interval)	χ^2	df	P
Coccidia score	110, 18	Urban	0.0097 (-0.011-0.031)	0.769	1	0.381
		Sex	0.1703 (-1.477-1.841)	0.162	1	0.687
		Body condition	-0.0721 (-0.138 to -0.009)	4.982	1	0.026
		Urban×sex	-0.0065 (-0.033-0.020)	0.233	1	0.630
Feather mite score	138, 18	Urban	0.0276 (0.009-0.049)	11.034	1	0.001
		Sex	0.9380 (-0.669-2.623)	0.226	1	0.635
		Body condition	0.0133 (-0.042-0.069)	0.222	1	0.638
		Urban×sex	-0.0129 (-0.038-0.011)	1.070	1	0.301

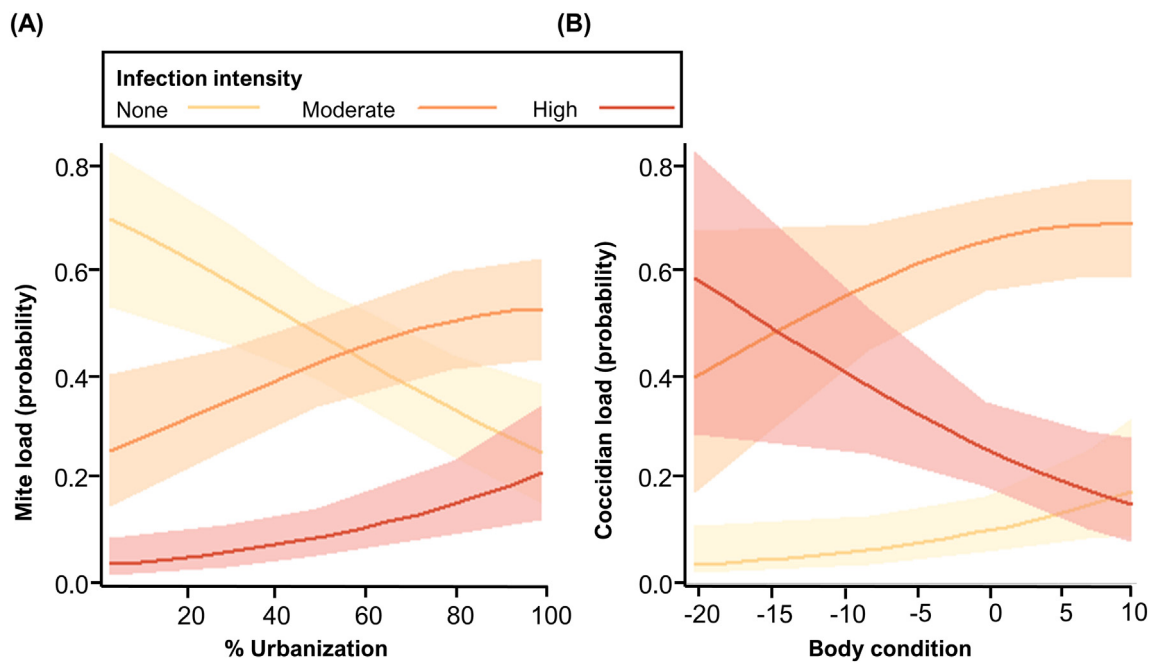


Fig. 3. Effect of % urbanization (A) and body condition (B) on the probability of no (yellow), moderate (orange), and high infection by feather mites or coccidia in common mynas. Model fit and 95% confidence intervals are shown.

Our results showed that mynas living under highly urbanized conditions had a significantly smaller niche than those conspecifics living in less urban surroundings. Furthermore, the overlap of high on low urban birds was greater than the overlap of low on high urban birds. This finding suggests that the foraging niche of highly urban mynas may be more restricted than the niche from individuals living in less urban areas, with urban birds consuming a narrower array of food sources. Nonetheless, consumer isotopic (δ -space) niche breadths are determined by both the number of foods consumed (diet diversity) and their relative separation in δ -space (isotopic variance) (Manlick et al., 2019; Newsome et al., 2007). Thus, differences in food source isotopic variance between low and high urbanized locations (e.g. due to more or less variable isotopic basal sources) could also potentially contribute to the observed pattern. Determining the isotopic signatures of

foods, and subsequently their proportional dietary contributions to mynas in low and high urbanized locations using Bayesian mixing models (Stock et al., 2018) would be a priority to further explore the effects of urbanized habitats on food intake and dietary breadth. If the differences in high and low urbanized niches are linked to accessing different types of resources in those environments, as suggested by the presence of foraging-related morphological adaptation in urban mynas (Magory Cohen et al., 2021), the narrower feeding niche of high urban mynas could be an indicator of poorer diet quality, as the intake of a lesser diversity of food types might restrict individual's ability to achieve their nutritional needs (Coogan et al., 2018; Nicholson et al., 2006; Votier et al., 2010). One possible explanation could be that birds from rural townships travel to areas beyond the urban matrix (Burstal et al., 2020) to access and forage on crop-eating arthropods in adjacent

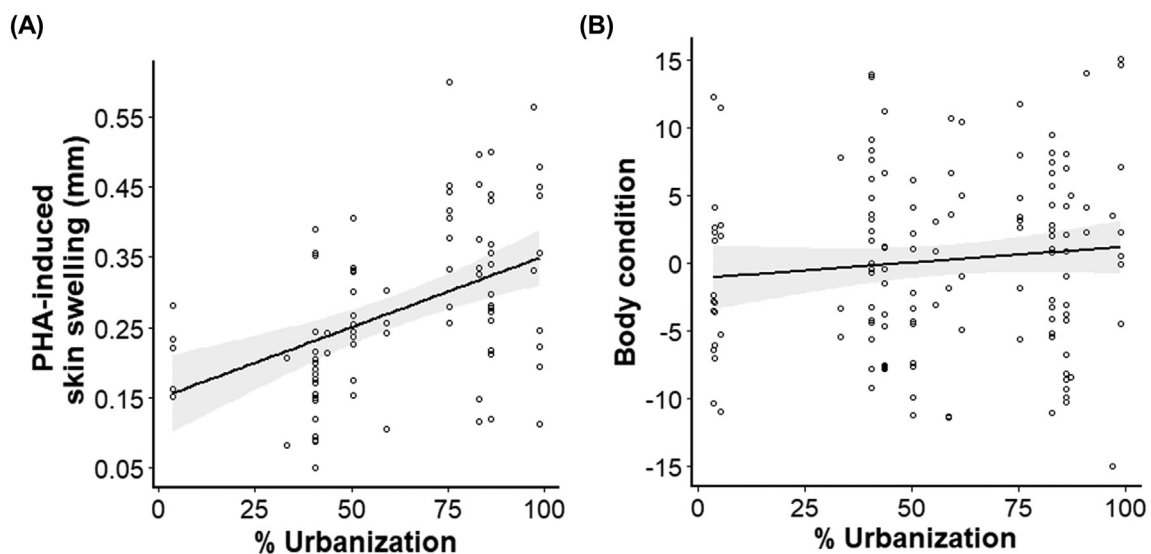


Fig. 4. Effect of % urbanization on PHA-induced skin swelling response (A) and body condition (B) in common mynas. Model fit and 95% confidence intervals are shown for the relationship with PHA ($p = 0.012$) and body condition ($p = 0.35$).

agricultural lands, as has been found in other species (Rose et al., 2006). Such food sources might be unavailable to mynas in highly urbanized areas and explain why mynas appear to be adapting morphologically (Magory Cohen et al., 2021). Overall, these results would suggest that birds outside urban centres might benefit from a more diversified and higher quality diet.

Analyses of morphological coloration provided convergent evidence that the diet of mynas outside urban centres might be of higher quality. Indeed, mynas displayed a more saturated, redder eye patch with a low UV component in areas with low build-up cover. Peneaux et al. (2020, 2021b) showed that eye patch coloration of mynas is formed by a combination of carotenoid pigments and microstructures and that coloration is severely reduced in response to dietary deficiencies in macronutrients and carotenoids, creating a possible link between poor nutrition and changes in coloration found here. This conclusion is consistent with previous work attributing decreased carotenoid-based coloration in urban birds to decreased quality, rather than quantity, of urban food sources (Hörak et al., 2000; Isaksson, 2009; Isaksson and Andersson, 2007; for a review see Peneaux et al., 2021a). For example, carotenoid content of trees can be lower in urban than in rural habitats, which in turn causes urban caterpillars to be poorer in carotenoids (Isaksson, 2009). In consistency with previous findings, body condition did not directly change as a function of urbanization level (Sumasgutner et al., 2018). Enhanced eye patch coloration of less urban birds was associated with higher body condition score, however. It is well established that carotenoid-based displays are honest signals of individual quality and health status in birds (Svensson and Wong, 2011; Weaver et al., 2018) and can reflect environmental quality (Peneaux et al., 2021a). In the light of this body of work on carotenoid-based morphological features in mynas and other birds, changes in eye patch coloration are consistent with reduced individual quality and health status in highly urbanized settings and suggest that urban habitats offer poorer nutritional environments for mynas than more natural environments.

Another potential indicator of poor living conditions was the finding that feather mites increased with urbanization levels. The prevalence and intensity of parasites and pathogens have been shown to increase in birds in highly urbanized habitats (Bradley et al., 2008; Delgado-V and French, 2015; Sykes et al., 2020). Parasites such as feather mites and coccidia can easily spread from one host to another by direct contact (physical or via an oral-faecal route) without the need for an intermediary (Dolnik et al., 2010; Proctor, 2003), making their infection rate likely to increase in densely populated urban environments where birds might be more prone to physical contacts (Bradley and Altizer, 2007). The increase in mite infestation in urban mynas could be explained by higher population densities in cities (Dyer et al., 2017a, 2017b; Grarock et al., 2014; Haythorpe et al., 2014; Lazarina et al., 2020; Old et al., 2014; Sol et al., 2012) coupled with the myna's communal roosting behaviour, both increasing the likelihood of direct physical contact between individuals (Counsilman, 1974). In contrast to feather mites, and despite mynas in poorer body condition being more likely to be heavily infected, coccidia infections rates were not higher in more urban mynas than in less urban areas. Absence of difference contrasts with several previous studies in birds (Delgado-V and French, 2015; Giraudeau et al., 2014; Sykes et al., 2020). Isosporan coccidia parasites are especially known for their association with reduced body weight, fertility and signal coloration, as well as poor nutrient resorption (Atkinson et al., 2008; Peneaux et al., 2021a), consistent with our finding that severely infected mynas were in poor body condition. However, parasite-host relationships are complex, and in the case of coccidia parasites, the prevalence and intensity of infection vary considerably among species and in response to species-specific foraging patterns (Dolnik et al., 2010), potentially explaining the lack of association with urbanization in our study.

The stronger swelling response following the injection of PHA in the wing web in more urbanized mynas indicates that immune

responsiveness can also be affected by urban ecological conditions. While it is now established that PHA induces both specific (T lymphocytes proliferation) and non-specific (heterophiles and monocytes phagocytosis) immune responses, the interpretation of these results in relation to health condition should be done with great caution (Kennedy and Nager, 2006; Vinkler et al., 2010). It seems that stronger swelling can be associated with either high-quality individuals being able to invest more resources and energy in immune defenses or diseased individuals with pre-activated immunity (Bílková et al., 2015; Peneaux et al., 2021a). For example, Audet et al. (2016) related strong immune responses in urban bullfinches (*Loxigilla barbadensis*) with a physiological adaptation of birds to urban environments and better immunocompetency. In most cases, the addition of other health- and quality-related parameters can facilitate the interpretation of PHA induced skin-swelling results (Bílková et al., 2015; Vinkler et al., 2012). When considering that more urban mynas were less coloured and more parasited with feather mites, it is possible that the stronger immune response indicate that urban mynas had pre-activated immunity and were in poor health (Bílková et al., 2015).

Many of the species studied in the context of urbanization have been natives that qualified as 'urban adapters' (Kark et al., 2007). These species often dwell in low disturbance areas such as woodlands, are not able to fully exploit urban environments, and have lower individual quality and poorer health in urban areas compared to natural habitats (Peneaux et al., 2021a). Our findings suggest that urban conditions might not be optimal even for an alien species considered an 'urban exploiter'. Throughout their introduced range, mynas show a strong association with urban cover and commonly use urban resources such as anthropogenic foods and breeding cavities in buildings (Khoury et al., 2021; Lowe et al., 2011; Machovsky-Capuska et al., 2016; Sol et al., 2012). For example, in Australia, myna population densities are highest in highly urbanized environments where native species abundance and diversity are lowest (Sol et al., 2012). However, this pattern of relative abundance is reversed at intermediate levels of urban cover (Sol et al., 2012). This selective occupancy is often interpreted as a habitat preference and underpins the conclusion that mynas pose little competitive risk to native birds due to this spatial segregation. Yet, it seems that ecological conditions in highly urbanized environments can also be detrimental to the health status and fitness of mynas, possibly driving range expansion to less densely occupied habitats.

While mynas might access higher quality habitats by island-hopping from a densely populated urban area to another less populated urban area, they might also reach essential resources by spreading from highly urbanized urban centres into spatially closer, more natural habitats (e.g., urban parks and natural bushland at the edges of cities), with the added benefit of avoiding the energetic costs and risks of long-distance travel. Consequently, colonizing parks and urban edges would likely increase spatial overlap and therefore competitive interactions with native species (Diquelou and Griffin, 2020). Direct observational evidence of aggressive competition for breeding resources has not yet been found in a large-scale nest-box study (Lermite et al., 2021; Rogers, 2018), although it has been inferred from patterns of nest box occupancy in remnant urban bushland in earlier work (Grarock et al., 2013; Pell and Tidemann, 1997). It has recently been shown that mynas are extremely aggressive around natural hollows (Rogers et al., 2020) and excluding them increases the breeding success of native species on islands (Blanvillain et al., 2020). If using resources in more natural environments depends upon phenotypical plasticity and/or natural selection for higher behavioural aggression, then identifying which urban living conditions are most detrimental and whether population hybridization is increasing genetic variation might help to predict where behavioural shifts are most likely to occur prior to a dispersion event (Ewart et al., 2019). Phenotypical shifts towards higher aggression and dispersal in response to a lack of breeding resources or detrimental environmental conditions have been found in other species (Aguillon and Duckworth, 2015; Duckworth and Badyaev, 2007; Hui

et al., 2012). Moreover, previous work has demonstrated a link between nutritional intake and exploratory phenotypes in mynas, pointing to the potential role of poor-quality urban foods in range expansion (Peneaux et al., 2017).

A better understanding of the developmental and environmental causes of aggression and exploration in mynas would be helpful in predicting potential shifts. Future research should also aim to explore to what extent possible morphological adaptations to foraging in cities found recently in mynas might create an evolutionary trap that offsets potential population shifts towards increased aggression and ties mynas inextricably to urban habitats (Magory Cohen et al., 2021).

5. Conclusions

In the present study, increasing levels of urbanization were associated with a smaller foraging niche, a decrease in signal coloration, higher ectoparasite loads and higher immune responsiveness. Together, these results suggest that mynas located in highly urbanized habitats might experience more detrimental living conditions than those living in less urbanized areas. Our findings are consistent with Shochat's (2004) theory, highlighting the impact of overcrowded urban habitats on the condition of avian populations. In alien invaders, the effects of deteriorating living conditions on population health could favour the apparition of range-expanding phenotypes and drive species spread. While mynas might island hop to new urban centres, the risk of this driving mynas to colonize remnant and suburban bushland, thereby increasing interactions with native birds, should not be disregarded.

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Ethical approval

All animal care and experimental procedures were in accordance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes and were approved by the University of Newcastle Animal Ethics Committee (protocol A-2017-718).

CRediT authorship contribution statement

Chloe Peneaux: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Visualization. **Richard Grainger:** Formal analysis, Writing – review & editing. **Françoise Lermite:** Methodology, Investigation, Formal analysis, Writing – review & editing. **Gabriel E. Machovsky-Capuska:** Writing – review & editing. **Troy Gaston:** Resources, Writing – review & editing. **Andrea S. Griffin:** Supervision, Conceptualization, Methodology, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

The program used in this study has been uploaded in Mendeley Data (doi: 10.17632/7zjdjt8dtk5.1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.148828>.

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