Biol Invasions (2020) 22:2525–2543
https://doi.org/10.1007/s10530-020-02269-7

ORIGINAL PAPER

Radiotracking invasive spread: Are common mynas more active and exploratory on the invasion front?

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Received: 16 June 2019 / Accepted: 28 April 2020 / Published online: 16 May 2020

Abstract Understanding the drivers of invasive species' range expansion is key to effective management and successful control. Spatial sorting theory advances that invasive species can spread via a selection-neutral process predicated on differential movement. In addition to morphology and physiology, it has been predicted that variation in exploration and activity among individuals can be crucial to this model because these behaviors enhance movement. We aimed to address the question of whether exploration and activity are associated with invasive spread using the free-ranging invasive common myna (*Acridotheres tristis*) in Australia, one of the most broadly distributed invasive birds globally. We radio-tracked mynas from invasion-front sites versus long-established sites in New South Wales. We quantified activity using frequent movements in familiar areas and exploration using infrequent long-distance excursive movements, while also accounting for environmental variation. We discovered that mean daily distance travelled was larger in invasion-front than in invasion-source mynas, suggesting front mynas were more active. Invasion front mynas had significantly larger exploratory home ranges, moved greater maximum daily distances, and changed roost more frequently, suggesting front mynas were also more exploratory; the results were maintained when climate was included as a covariate. To our knowledge, this is the first study to show enhanced exploration and activity in free-ranging invasion-front birds. Inter-individual variation in movement-relevant behaviors might be facilitating the ongoing Australian myna range expansion, although habitat effects cannot be fully excluded. These findings point to the potential importance of considering changes in behavior when modelling alien animal invasions and applied conservation actions.

Keywords Activity behavior · Common/Indian myna · Exploration behavior · Invasive alien birds · Movement · Radiotracking

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Introduction

Understanding the causes, consequences and dynamics of invasive species' range expansion is critically important to effective management and successful control (Pimental et al. 2000). In the last decade, substantial attention has been given to the possibility that range expansion in invasive species involves a run-away, selection neutral process predicated on differential movement (Hastings et al. 2004; Phillips et al. 2006, 2007; Rollins et al. 2015; Hudson et al. 2016; Cobben et al. 2017; Gruber et al. 2017; Ochocki and Miller 2017; Weiss-lehman 2017; Weiss-Lehman et al. 2017). The process, referred to as spatial sorting, results from morphological (e.g., wing length), physiological (e.g., endurance) or behavioral (e.g., exploration) differences that allow some individuals to move further than others across the landscape coupled with the subsequent inter-breeding of these spatially contiguous, fast-moving individuals (Alford et al. 2009; Llewelyn et al. 2010; Berthouly-Salazar et al. 2012; Liebl and Martin 2012; Lindström et al. 2013; Therry et al. 2014; Louppe et al. 2017).

The idea that range expansion in invasive species can be effectively selection neutral is at odds with strongly established thinking within the animal dispersal literature. There, dispersal is considered to constitute a life-history trait shaped by its costs and benefits (Clobert et al. 2004, 2009; Cote et al. 2010a; Bonte et al. 2012; Duckworth 2012; Travis et al. 2012). In wild populations, it is well known that individuals differ significantly in the likelihood and distance of dispersal (Dufty and Beltoff 2001; Fidler et al. 2007; Cote et al. 2011; Quinn et al. 2011; Korsten et al. 2013; Wey et al. 2015; Michelangeli et al. 2017). In some cases, such variation is explained by viewing dispersal and philopatry as differential investment strategies in phenotypic and life history traits that might ultimately achieve the same fitness. For example, individuals with so-called 'dispersing syndromes' invest in morphological and physiological adaptations that minimise the costs of dispersal and maximise the chances of successful settlement in new areas (Debeffe et al. 2013, 2014; Stevens et al. 2013). Patterns of correlations between dispersal and behavioral, physiological and morphological traits might be influenced by environmental variation through space (Clobert et al. 2009; Cote et al. 2010b; Ramanantoanina and Hui 2015). For example, in habitat matching, a phenotype's fitness depends upon environmental conditions and each phenotype makes an adaptive decision to disperse from its less favourable habitat towards its most favourable habitat (Travis et al. 2012). In other cases, dispersal behavior is a conditional response to environmental cues such as habitat quality, rearing conditions and local population density. For example, increases in population density can trigger maternal manipulation of offspring phenotype giving rise to offspring with greater dispersing tendencies (Duckworth 2009). Here, the act of dispersal is considered the end-result of an information gathering exercise—the concept of 'informed dispersal' (Clobert et al. 2009). Whether the mechanisms of dispersal (and therefore range expansion) in invasive species differ fundamentally and systematically from those of non-invasive species (selection-neutral versus adaptive) is not known.

A common research paradigm to examine the traits associated with invasive range expansion involves comparing the phenotypes of individuals on the front of an invasion wave with those on the back, or core of an invasion wave (Duckworth and Badyaev 2007; Liebl and Martin 2012, 2014; Lindström et al. 2013; Martin 2014; Gruber et al. 2017; Louppe et al. 2017). Such research is yielding increasing support for invasive spread by spatial sorting by demonstrating strengthened morphological and physiological dispersal-relevant traits in individuals at invasion fronts (Simmons and Thomas 2004; Leotard et al. 2009). For example, invading speckled wood butterflies (*Pararge aegeria*) at the invasion front have larger thoraxes (to accommodate larger flight muscles), smaller abdomens (to reduce weight), and larger wings (to increase the wing loading), all of which facilitate increased dispersal distances (Hugues et al. 2007). In amphibians, invasive cane toads (*Rhinella marina*) at the invasion front have longer legs (Phillips et al. 2006), grow faster (Phillips 2009), and have greater endurance (Llewelyn et al. 2010) than their conspecifics in the range core. These morphological and physiological shifts have been associated with a fivefold increase in the toads' rate of range expansion (Phillips et al. 2006, 2007). Recent experimental assays and modelling approaches have confirmed that the process of spatial sorting alone can lead to increased dispersal tendency and generate accelerating invasion edges (Ramanantoanina et al. 2014; Ochocki and Miller 2017).

Activity refers to general levels of activity in familiar, safe environments (Dingemanse et al. 2007; Carter et al. 2013). Exploration behavior refers to the gathering of information about objects and places that does not satisfy immediate needs and, when applied to space, is generally considered to encompass (more rare) movements into, and within unfamiliar surroundings (Dingemanse et al. 2002, 2007; Mettke-Hofmann et al. 2002, 2009; Matzel et al. 2006; Réale et al. 2007; Carter et al. 2013; Gordon et al. 2014; Huang et al. 2016; Perals et al. 2017). Inter-individual variation in activity and exploration are considered to form a personality syndrome (Cote et al. 2010b), which predicts dispersal tendency and patterns in a diverse range of taxa (Dingemanse et al. 2003; Haughland and Larsen 2004; Alford et al. 2009; Hoset et al. 2011; Debeffe et al. 2013; Sol et al. 2013; van Overveld et al. 2014; Thorlacius et al. 2015). There is also evidence for a genetic integration of heritable variation in exploration and dispersal distances in birds (Korsten et al. 2013). Exploration and activity are hence two behaviors that could influence how fast an animal moves across a landscape, but so far, evidence for their strengthened expression in individual animals at invasion fronts is mixed (Cote et al. 2010b; Liebl and Martin 2012; Michelangeli et al. 2016; Gruber et al. 2017; Felden et al. 2018). In amphibians, individual cane toads at the invasion front are more active and move in straighter paths than their conspecifics in the core range (Alford et al. 2009), and they are also more exploratory (Gruber et al. 2018). In birds, invading house sparrows (*Passer domesticus*) from invasion fronts are more exploratory (Liebl and Martin 2012), but they also consume novel foods more quickly (Liebl and Martin 2014), a trait unrelated to dispersal. In addition, Felden et al. (2018) found no evidence of an association between invasiveness and within-species variation in activity in invasive Argentinian ants (*Linepithema humile*). Given this small body of work and its mixed findings, the next logical step to determining whether movement-relevant behavior is implicated under some conditions and not others in the range expansion of invasive species requires broadening the range of alien animal species under study (Fogarty et al. 2011; Lee 2011; Truhlar and Aldridge 2015). The present work therefore aimed to examine whether movement-related behaviors are involved in the Australian range expansion of one of the most successful invasive birds globally, the common (Indian) myna (*Acridotheres tristis*).

The common myna is a medium-sized communal passerine that has experienced global spread (IUCN Global Invasive Species Database 2015) (Martin 1996; Lim et al. 2003; Holzapfel et al. 2006; Peacock et al. 2007; Saavedra et al. 2015; Engel and Willard 2017; Ewart et al. 2018; Magory Cohen et al. 2019) and is one of only three avian species to be listed by the IUCN as being among 100 of the world's most invasive species (Lowe et al. 2000). The myna was first introduced into Australia in the early 1860s (McCoy 1885) and through a series of human-assisted translocations and range expansions is now the most common bird species in major urban centers along Australia's eastern coastline (Sol et al. 2012; Ewart et al. 2018). Historical atlas data as well as genetic analyses indicate that the common myna is currently undergoing a range expansion westward from the coast (Ewart et al. 2018) (Atlas of Living Australia website http://www.ala.org.au). One possible model of range expansion is that mynas spread by spatially segregating along variation in a dispersal-relevant trait. Support for spatial sorting has been gathered from analyzing wing morphology within the South African range expansion and showing that wing length increases with distance from the point of introduction (Berthouly-Salazar et al. 2012). Here, we extend this work by examining whether radio tracked, free-ranging invasion-front mynas also display changes in dispersal-relevant behaviors, namely exploration and activity, relative to mynas from long-established source areas. Invasion front/source differences in exploration and activity would be in line with a spatial sorting model of range expansion, whereas an absence of difference would direct attention to alternative models of range expansion based on adaptive dispersal, such as habitat matching (Clobert et al. 2009).

Materials and methods

Study locations

We quantified spatial movements of common mynas in NSW, eastern Australia, across two recently established front populations and two long-established source populations using radiotracking. Recently established populations were within the rural towns of Gloucester (− 32.0272, 151.9602) and Bulahdelah

(– 32.4044, 152.2097) on the western edge of the common myna's NSW invasion wave, where data from the Atlas of Living Australia indicates that mynas have only begun breeding within the last 15 years. Long established populations were found in the suburbs of Tighes Hill (– 32.9048, 151.7575) and Hamilton South (– 32.9307, 151.7511) of the city of Newcastle where common mynas have been breeding since 1975 (Hone 1978). Study sites were selected so as to match urban density as closely as possible at a local scale (< 1 km^2) (Fig. 1), but this was not possible at a wider scale (> 4 km^2) (Fig. 2). This is because common mynas are spreading from large coastal cities to smaller inland townships where urban habitat subsides more quickly to rural habitat (Ewart et al. 2018). Mynas are widely considered to be relatively sedentary (Kang 1992; Berthouly-Salazar et al. 2012; Ewart et al. 2018), are mostly restricted to urban habitats (Crisp and Lilli 2006; Lowe et al. 2011; Sol et al. 2012; Haythorpe et al. 2014; Old et al. 2014), with previously reported core (routine) home range sizes of ~ 0.1 km^2 (Kang 1989, 1992), so habitat-matching at a local scale is likely to be biologically justified for this species.

We captured 24 adult common mynas (six from each study location) from the wild using walk-in baited traps. We weighed each bird and measured its beak, wing, and tarsus. Male and female common mynas cannot be distinguished on the basis of plumage. Although males are larger than females, the distribution of male and female dimensions overlap considerably (Old et al. 2014). Consequently,

Fig. 1 Satellite images of the trapping locations and their 1 km^2 surroundings retrieved from Google Earth Pro. Source locations (left side): Tighes Hill (trap location: – 32.9048, 151.7575) (top panel); Hamilton South (– 32.9307, 151.7511) (lower panel). Front locations (right side): Bulahdelah (trap location: – 32.4044, 152.2097) (top panel); Gloucester (trap location: – 32.0272, 151.9602) (lower panel). The red lines indicate a 0.5 km distance north, east, south and west from the trap. The intersection of the four red lines indicates the trap location

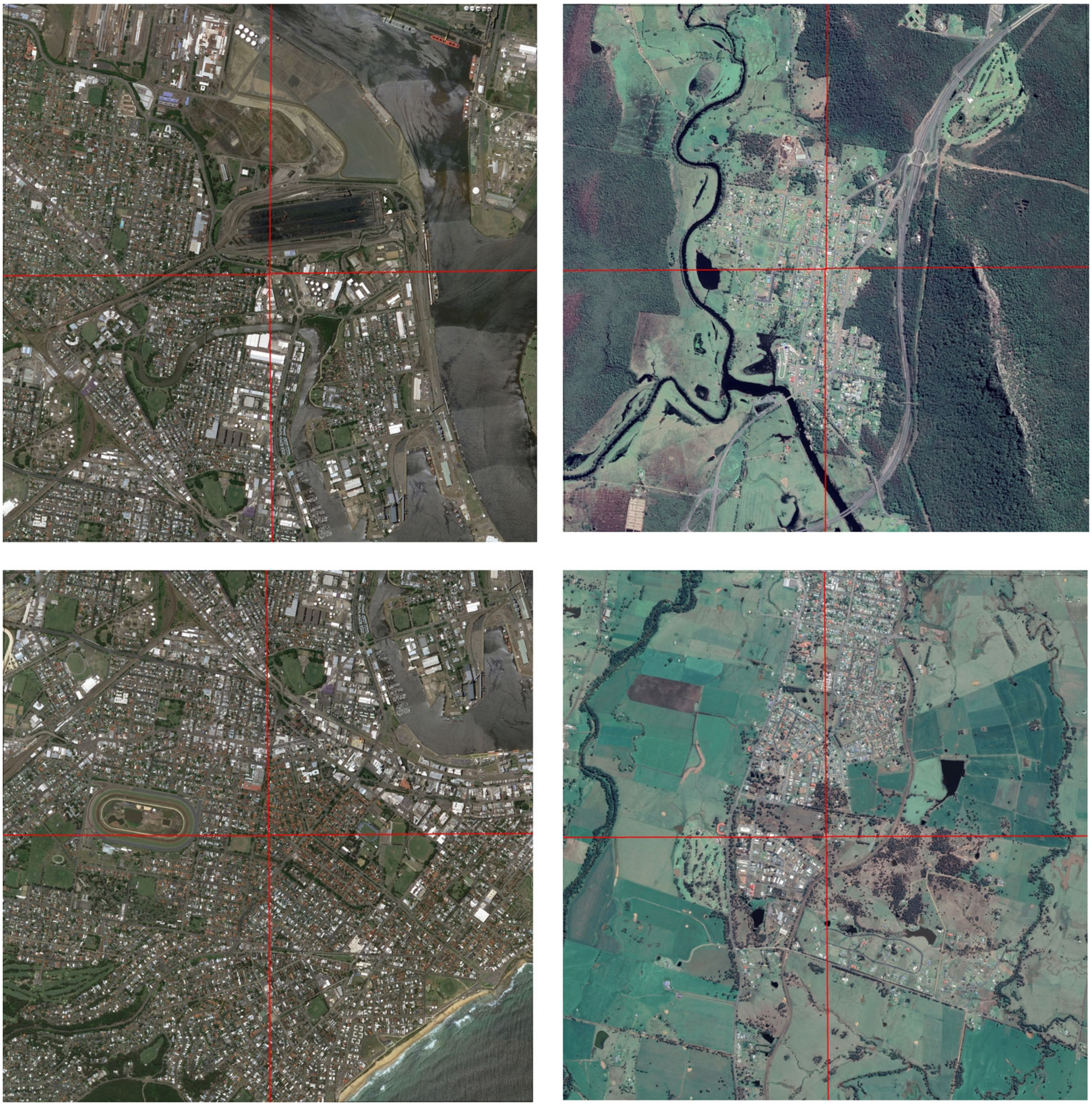

Fig. 2 Satellite images of the trapping locations and their 16 km^2 surroundings retrieved from Google Earth Pro. Source and front locations are depicted as per Fig. 1. The red lines indicate a 2 km distance north, east, south and west from the trap. The intersection of the four lines indicates the trap location

we collected a feather for sexing via DNA analysis. At the time of capture and tagging, we attempted to balance the sex ratio of the sample on the basis of an educated guess as to the birds' sex. To avoid age effects, we excluded juvenile birds from the sample by not selecting birds with a juvenile brown plumage.

At the time of capture, we fitted each bird with a unique combination of colored leg bands to allow for long-distance visual identification of individual birds, as well as a radio transmitter (details below). Two birds' transmitters failed or fell off before meaningful data could be collected. The final sample size was therefore 22 birds; 11 from front, recently established populations (three females and eight males), and 11 from source, long established populations (six females and five males). Although our final sample size is small relative to the sample sizes used for front/source comparisons using captive-held birds (Liebl and Martin 2012, 2014), it is within the typical range of sample sizes for hand-held telemetry studies on free-ranging birds (Kubiczek et al. 2014; Tingley et al. 2014; Loretto et al. 2015; Habel et al. 2016; Real et al. 2016; Rechetelo et al. 2016; Cunningham et al. 2016; Kolts and McRae 2017). Further, there is need to make sure expensive, labour-intensive radio-tracking movement data are disseminated (Campbell et al. 2015).

Radiotracking methods

At the time of capture, we fitted each bird with a 2.4 g single stage transmitter with a 15-cm stranded antenna and a battery life of approximately 6 weeks (Ultimate Lite VHF transmitter model V1G 112A, Sirtrack). We attached the transmitters to the birds using Rappole style harnesses (Rappole and Tipton 1991), which cause minimal discomfort to the bird (Rappole and Tipton 1991; Woolnough et al. 2004) and have been shown to be significantly more reliable in terms of attachment duration than other attachment methods such as gluing the tag directly onto the bird's feathers (Woolnough et al. 2004). We sized the harnesses using the Naef-Daenzer (2007) method, and fastened them using a reef knot strengthened with a drop of cyanoacrylate glue. This method of fastening was chosen over other methods (like sewing) because it has been found to maximize the likelihood of eventual harness failure, thus allowing the birds to shed the harnesses after the transmitter has run out of battery (Herring and Gawlik 2010). This did indeed happen, with many of the birds shedding their harness after about 5 weeks. The mass of the harness and radio-transmitter was approximately 3 g. Since the average weight of adult common mynas from the NSW Hunter region is 112 g (A. S. Griffin, unpublished data), our harnesses satisfied the requirement of the Animal Research Review Panel's wildlife research guidelines that the weight of a mounted transmitter is ideally less than 5% and no greater than 10% of the weight of the animal (Animal Research Review Panel 2015).

We conducted radiotracking over two successive 6-week periods during the months of May to August, which corresponds to the non-breeding season of mynas in Australia. Birds from one long—(Tighes Hill) and one recently—(Gloucester) established population were tracked in the first 6-week tracking period, while birds from the other long—(Hamilton South) and recently—(Bulahdelah) established populations were tracked during the second 6-week period. The collection of data was split into two 6-week periods because it was logistically not possible to track all 22 birds simultaneously.

To gather as much spatial data as possible while in the field, we aimed to track each bird continuously for 1 day per week for the entire 6-week period. Due to early tag detachment or early battery failure, the number of tracking days per bird varied from 2–6 days (mean 5.1 ± SE 0.3). In a given location, we recorded successive spatial positions of between two and four (but typically three) birds on any given tracking day beginning around 8 am and ending at dusk. Each bird was located at least five times per day, including once in the roost at dusk. The birds' positions were recorded serially, in an order that was randomized each day to minimize temporal autocorrelation (Kenward 2001). The total number of location fixes across the entire tracking period ranged from 16 to 59 fixes per bird (mean 42.4 ± SE 2.9).

The birds were located using a combination of homing and triangulation. The general vicinity of the bird was first located by vehicular tracking using a roof-mounted 148–175 MHz monopole whip antenna (RFI Wireless) attached to a Regal 2000 Telemetry Receiver (Titley Scientific). If the signal from the roof-mounted antenna was very strong, we attempted to sight the bird from within the vehicle using binoculars. If the bird was successfully sighted, then we recorded its location either directly by taking a GPS location (if its location was in a public, approachable place), or indirectly by triangulation (if its location was on private or inaccessible land).

If the signal from the roof-mounted antenna was not very strong, or the bird could not be sighted, the bird was tracked on foot using a handheld Yagi three-element 151 MHz antenna attached to a Regal 2000 Telemetry Receiver (Titley Scientific). The signal was followed for as long as possible until the bird was sighted and its location recorded as above. If the bird could not be sighted despite tracking on foot, then its location was identified by triangulating.

To minimize error when triangulating, all three bearings were recorded within a 10-min period, the overall angular difference between the two outside bearings was kept between 60° and 120°, and the angular differences between the middle bearing and the two outside bearings was kept to more than 20° (Kenward 2001). We took bearings using a magnetic compass, and the locations from which bearings were recorded in UTM were identified using a Magellan eXplorist 110 GPS (accuracy 10 m). We also recorded the locations of any opportunistic sightings of a tagged bird identified on the basis of its coloured leg bands (see above).

Behavioral variables

Overview

Raw triangulation data were converted into a list of estimated location points with error ellipses for each bird using the computer program Locate III (Nams 2011). Point sightings were added manually. We assigned point sightings a circular error ellipse with a radius of 10 m, as this was the accuracy of the GPS we used to record the point sightings. We then used these data to calculate several distinct variables describing exploration and activity.

Some authors differentiate between activity and exploration by considering all movements per se as activity and exploration as area covered while moving (Cote et al. 2010b, 2011). However, the more widespread view is that activity reflects general levels of activity in routine, familiar environments (e.g., Dingemanse et al. 2007; Carter et al. 2013) and is typically calculated as movement frequencies in captive novel environment exploration assays (Galsworthy et al. 2005; Lermite et al. 2017). In contrast, exploration encompasses (more rare) movements into, and within unfamiliar surroundings and is most often quantified as latencies to land in new areas in standardized novel environment exploration assays (e.g., Dingemanse et al. 2007; Mettke-Hofmann et al. 2009; Huang et al. 2016). Drawing upon these activity/exploration distinctions outlined in the literature, we considered as activity variables ones that quantified common movements within a routine area of usage (i.e. core home range size), general levels of activity (i.e. mean distance moved per move), and frequency of movements (i.e. probability of moving). We considered exploration variables ones that quantified rarer movements outside the routine area of usage (i.e. exploratory home range size, maximum daily distance moved). We also assumed that a more exploratory bird would use a greater number of different overnight roosts. Details of how these variables were quantified are described next.

Activity

Core home range size We calculated the core home range size for each bird using the 50% isopleth of the kernel density estimation (KDE) (Worton 1989). A KDE uses the relative density of an individual's location points to estimate how frequently the individual visits different areas. The 50% inner isopleth of a KDE bounds the area in which the individual spends 50% of its time, and is often referred to as the core home range (Mabry and Pinter-Wollman 2010). The size of the core home range measures the size of the individual's most frequently used areas, and thus represents the extent of the individual's routine exploratory behavior over the time that it was tracked (Minderman et al. 2010).

We generated the KDEs in ArcGIS Desktop v10.3 using the Kernel Density tool in the Spatial Analyst toolbox (ESRI 2015). The output resolution was set at 5 m by 5 m. We chose the bandwidth (also known as the smoothing parameter, search radius or h) for each individual's KDE using Silverman's 'subjective choice' method, which is to "plot out several curves and choose the estimate that is most in accordance with one's prior ideas about the density" (Silverman 1986). The choice of bandwidth has considerable influence over the size and shape of the resulting KDE, and there are many methods for selecting which bandwidth to use (Worton 1989; Seaman and Powell 1996). We elected to use the selective choice method because the majority of individuals had a strongly multimodal distribution of points and had fewer than 100 location points—thereby rendering automatic methods unsuitable. In addition to this, the data were inherently suited to the subjective choice method because extensive time spent in the field during data collection meant that detailed and well informed prior ideas about density were available to guide the choices (Silverman 1986).

For each bird, we first generated a trial KDE using a bandwidth of 100 m. If the trial KDE appeared to be under-smoothed (e.g., unimportant features were prominent), the bandwidth was increased in intervals of 25 m until a realistic surface was achieved. Similarly, if the trial KDE appeared to be over-smoothed (e.g., important features were obscured), the bandwidth was decreased in intervals of 25 m. If the trial KDE already appeared to be realistic, the bandwidth was increased and decreased by at least two 25-m intervals in each direction to confirm that a more realistic surface could not be achieved. Our final bandwidths varied from 75 to 325 m, with the majority around 125 m. Once we had found the most realistic KDE for each individual, we extracted the area of the core home range by classifying the KDE into ten equal percentage classes, splitting the ten classes into two sections—the inner 50% and the outer 50%, and then taking the area of the inner 50% section.

Mean distance moved per move We calculated the mean distance moved per move as being the total daily distance moved divided by the number of movements made, where the total daily distance moved was the sum of the Euclidean distances between all consecutive location points in a day. We did not include instances where the bird remained in exactly the same location for consecutive location points.

Probability of moving We calculated the probability of moving as being the number of times the bird had moved from its previous locality divided by the total number of times it was located (Alford et al. 2009). We considered the bird to have moved from its previous locality if it had moved a distance of more than 80 m. This threshold was selected because field observations indicated that 80 m corresponded to the typical minimum distance between different foraging areas. We excluded the final movement of each day into the roost from this calculation because it reflected the time of day (nightfall) rather than the underlying activity levels of each bird.

Exploration behavior

Exploratory home range size We calculated the exploratory home range size for each bird using the size of the minimum convex polygon (MCP), which is the polygon formed by joining the outermost location points of an individual. These outermost points capture rare long-distance excursions made by the individual, and thus the size of the MCP represents the maximum extent of the individual's excursive exploratory behavior over the time period that it was tracked (Minderman et al. 2010). We generated the MCPs in ArcGIS Desktop v10.3 using the Minimum Bounding Geometry tool in the Data Management toolbox (ESRI 2015).

Maximum daily distance moved We defined the maximum daily distance moved by each bird as being the largest distance between any pair of an individual bird's location points in the same day, whether they be consecutive or non-consecutive. We therefore calculated the maximum daily distance moved as the Euclidean distance between the two most distant locations. We used maximum daily distance to represent the extent of day-to-day exploration for an individual.

Number of overnight roosts We defined the number of overnight roosts as the number of different roosts (typically trees) in which we located an individual at the last positional fix of the day, typically just before sunset. If an individual changed roosts only to return to the old roost at a later date, we did not re-count the old roost.

Environmental variables

Temperature and rainfall

Possible effects of climatic conditions were taken into account by measuring temperature and rainfall for each tracking day. For the first tracking period, the maximum temperature for each tracking day was recovered from the Bureau of Meteorology (BOM) records from the nearest weather station to each study site (http://www.bom.gov.au/nsw/), whereas for the second period of tracking, the maximum temperature experienced during tracking was recorded. We recorded daily rainfall totals from the closest BOM rainfall station to each study site (http://www.bom.gov.au/nsw/).

Species diversity and abundance

In order to account for possible effects of local bird abundances on myna movement behavior, we collected data on common myna population density, total avian density, and avian diversity at each study location using point-counts (Hamel et al. 1996). We conducted point-counts twice at each trapping location, once at the start of the 6-week tracking period and again at the end. To conduct a point count, we waited for 5 min after arriving at the trapping site to allow birds to adjust to our presence. For a period of 10 min, we then proceeded to identify both visually and aurally all bird species present within a 50 m radius of the trapping site, and recorded their abundance. We used the counts to calculate common myna density and total avian density for each trapping location. The total number of different species that were observed during the two point-counts was used as a measure of avian diversity.

Statistical analyses

Linear models (LMs) were fitted to spatial movement measures that were calculated once for each bird across the entire tracking period (‘summary spatial movement variables’) (core home range size, exploratory home range size, number of roosts). Linear mixed models (LMMs) including bird ID as a random factor were fitted to the means of each of the daily spatial movement variables, which were calculated each time a bird was tracked for a full day (maximum daily distance moved, mean distance moved per move, probability of moving). Invasion stage, sex, season and study location were included as fixed factors in all models. Several covariates, namely common myna population density, maximum temperature and total rainfall, were examined using an analysis of covariance approach in which parallel and different slopes were tested. For models of summary movement variables, a maximum temperature value for each bird was obtained by averaging all measurements of maximum daily temperature recorded each day the bird was tracked. Equally, rainfall was calculated as the total of all rainfall values recorded across all days the bird was tracked. Total bird population density and bird diversity were not included in any model because these variables were highly correlated with common myna population density, so including them created problems of collinearity amongst predictor variables.

For each spatial movement variable, a Minimum Adequate Model (MAM) containing only significant effects ($\alpha = 0.05$) was identified using a stepwise procedure. First, the most suitable covariance structure was identified by testing the suitability of different covariance structures and groupings using the Akaike Information Criterion (AIC) (Akaike 1974). We interpreted a reduction of more than two points to indicate a significantly improved model fit (Burnham and Anderson 2004). Testing of the different covariance structures was conducted on a base model where invasion stage, the predictor of primary interest, was included as the only explanatory variable. For LMMs, we tested two covariance structures, namely a compound-symmetry and a first-order auto-regressive. For both LMs and LMMs, we compared the fit of models with and without variance grouped by invasion stage.

The remaining predictor variables were then added into the best-fitting base model to form a full model. Residual plots of the full model were examined for constant variance and normality of residuals, and, if needed, the dependent variable was log-transformed to improve fit. The full model was then progressively simplified using stepwise deletion of non-significant effects ($\alpha = 0.05$) until only significant main effects remained. If the effects of several predictor variables were non-significant at a given step, the least significant term was removed first. Invasion stage was not deleted even if it was non-significant, since it was the primary predictor of interest. Finally, interactions between the remaining predictor variables were tested one by one by adding the single interaction term to the model with its main effects. All interactions that had been significant were then added into the simplified model. If necessary, the model was simplified once again through stepwise deletion of non-significant interaction terms until only main effects and significant interactions remained. At this point, the model was considered to have reached the MAM. We checked the residual plots of the MAM to verify that the assumptions of constant variance (for all data or within variance groups) and normality of residuals were still satisfied. Effect sizes were calculated as differences based on estimated marginal means, or, if log transformations of the outcome variable had been used, the exponential of differences of marginal means (‘response ratios’; Borenstein et al. 2009). All analyses were conducted using the GLIMMIX procedure in SAS Version 9.4.

Ethical statement

All applicable institutional and/or national guidelines for the care and use of animals were followed. All procedures were approved by the University of Newcastle Animal Care and Ethics committee, protocol number A-2011-154.

Results

Activity

Core home range size Both invasion stage and the interaction between invasion stage and sex were significant predictors of core home range size (Table 1). Overall, core home ranges were larger in front populations than they were in source populations (Table 2). Females in source, long-established populations had larger core home ranges than males, whereas females in recently established populations had smaller core home ranges than males (Table 2, Fig. 3). The effect sizes of the interaction terms were considerably smaller than the effect size of invasion stage (Table 2). We found no correlation between the number of times a bird was located and the size of its core home range (Pearson's correlation, $r = -0.05$, $N = 22$, $P = 0.819$).

Mean distance travelled per move Invasion stage, conspecific density and the interaction between the two were all significant predictors of mean distance moved per move (Table 1). Overall, the mean distance moved per move was about 63% greater in birds at the invasion front than in birds at the invasion source (Table 2). For every one unit increase in the conspecific population density the mean distance moved per move decreased by around 6% in mynas in new populations, but increased by around 17% in mynas in old established populations. Although not significant, there was some evidence of a significant negative correlation between the number of times a bird was located and mean distance travelled per move (Pearson's correlation, $r = -0.38$, $N = 22$, $P = 0.08$). Three of four birds with the lowest number of fixes were source birds, however, meaning that, if anything, fewer fixes biased against our hypothesis that front birds would be more active.

Probability of moving Probability of moving was not significantly affected by invasion stage or by any other covariate (Table 1). The probability of moving was 0.66 (95% CI [0.59, 0.73]) in mynas in source populations and 0.60 (95% CI [0.52, 0.67]) in mynas in source populations.

Exploration

Exploratory home range size Invasion stage was a significant predictor of the size of the exploratory home range (Table 1). Mynas at the invasion front had

Table 1 Minimum adequate models (MAM) explaining variation in myna movement variables

Outcome (movement) and predictor variables	*df*	F	*p*
Activity			
Core home range size[a]			
Invasion stage	1, 18	43.95	< 0.001
Sex	1, 18	0.25	0.616
Invasion stage × sex	1, 18	41.96	< 0.001
Mean distance travelled per move[a]			
Invasion stage	1, 18	41.68	< 0.001
Conspecific population density	1, 18	6.02	0.025
Invasion stage × density	1, 18	33.11	< .0001
Probability of moving			
Invasion stage	1, 20	1.94	0.179
Exploration			
Maximum daily distance moved			
Invasion stage	1, 19	5.34	0.032
Sex	1, 19	3.50	0.077
Exploratory home range size[a]			
Invasion stage	1, 19	75.02	< 0.001
Number of overnight roosts[a]			
Invasion stage	1, 20	100.83	< 0.001

N = 22 for all analyses. Tracking day was used to form a residual covariance structure in the analyses for maximum daily distance moved, mean distance moved per move and probability of moving

[a] The outcome variable was log-transformed

Table 2 For each outcome variable, significant effects in MAMs were estimated as marginal means

Outcome (movement) variable	Effect	Level	Mean	95% CI		Effect size	95% CI	
				Lower	Upper		Lower	Upper
Core home range size (km^2)[a]	Invasion stage	Front	0.031	0.027	0.037	2.06	1.66	2.56
		Source	0.015	0.013	0.018			
	Invasion stage × sex	Front F	0.021	0.016	0.027	0.47	0.34	0.64
		Front M	0.046	0.039	0.054			
		Source F	0.021	0.016	0.026	1.92	1.42	2.59
		Source M	0.011	0.009	0.013			
Mean distance moved per move (m)[a]	Invasion stage	Front	277	220	347	1.63	1.23	2.14
		Source	170	145	198			
Exploratory home range size (km^2)[a]	Invasion stage	Front	0.66	0.50	0.87	5.53	3.66	7.91
		Source	0.12	0.09	0.16			
Maximum daily distance moved (m)	Invasion stage	Front	1058	801	1315	389	37	742
		Source	669	429	908			
	Sex	Female	1024	749	1299	321	− 38	680
		Male	703	479	926			
Number of roosts[a]	Invasion stage	Front	2.4	2.1	2.8	2.1	1.8	2.5
		Source	1.2	1.1	1.3			

All variables were log-transformed for analyses except Maximum daily distance moved. Effect sizes were calculated as differences based on estimated marginal means, or, if log transformations of the outcome variable had been used, the exponential of differences of marginal means ('response ratios'; Borenstein et al. 2009)

[a] The outcome variable was log-transformed

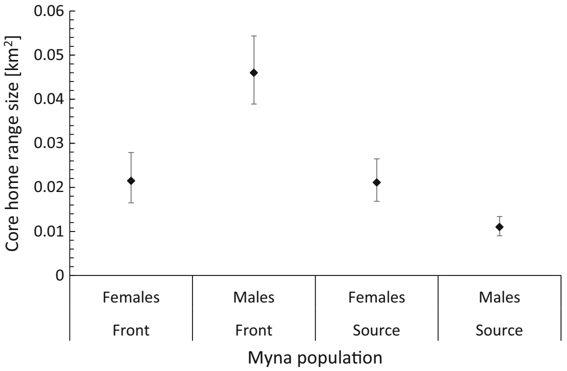

Fig. 3 Core home range size (mean ± 95% CI) of male and female common mynas in recently-established, invasion front and long-established, source populations. Depicted means represent marginal means from MAMS (Tables 1 and 2)

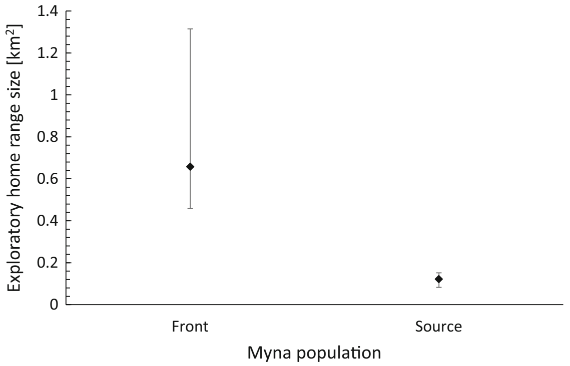

Fig. 4 Exploratory home range size (mean ± 95% CI) of common mynas in recently-established, invasion front and long-established, source populations. Depicted means represent marginal means from MAMS (Tables 1 and 2)

exploratory home ranges that were more than 5.5 times larger than mynas at the invasion source (Table 2; Fig. 4). Exploratory home ranges were ∼ 9 times larger than core home ranges in source populations, but ∼ 21 times larger than core home ranges in front populations (Table 2). There was no correlation between the number of times a bird was located and the size of its exploratory home range (Pearson's correlation, $r = -0.01$, $N = 22$, $P = 0.963$).

Maximum daily distance moved Invasion stage was a significant predictor of maximum distance moved by mynas each day (Table 1). Mynas in front populations moved significantly greater distances each day than birds in source populations (Table 2; Fig. 5). Sex was a marginally significant predictor of maximum daily distance moved with females tending to move greater maximum distances each day than males (Table 2). The effect of invasion stage was larger than that of sex (Table 2). There was a significant negative correlation between the number of times a bird was located and maximum daily distance moved (Pearson's correlation, $r = -0.45$, $N = 22$, $P = 0.036$). Three of four birds with the lowest number of fixes were source birds, however, meaning that, if anything, fewer fixes biased against our hypothesis that front birds would be more exploratory.

Number of roosts Invasion stage was the only significant predictor of the number of roosts (Table 1). Birds at the invasion front had twice the number of roosts than birds at the invasion source (Table 2).

Discussion

Despite a long-standing general interest in the role of inter-individual behavioral variation in dispersal (reviewed by Wey et al. 2015), it is only in the last decade that significant attention has been paid to how variation in 'dispersal-relevant' behavior can facilitate the spread of invasive alien species (e.g., Alford et al. 2009; Chapple et al. 2012; Liebl and Martin 2012; Thorlacius et al. 2015). Here, we examined the association between exploration, activity and invasion stage in free-ranging invasive common mynas in Australia. Based on considerations that (1) South African mynas are spreading by spatially sorting along a gradient of inter-individual variation in a dispersal-enhancing morphological trait (wing length) (Berthouly-Salazar et al. 2012), and that (2) exploration and activity are linked to dispersal (e.g., Clobert et al. 2009; Liebl and Martin 2012; Korsten et al. 2013), we predicted that birds from invasion front populations would be more exploratory and more active than their counterparts in long-established populations. We attempted to tease apart activity from exploration by considering common, day-to-day movements within a routine area of usage as activity, and rarer movements outside the routine area of usage as exploration. This distinction drew upon the large behavioral literature on activity and exploration, which considers activity to represent routine movements in familiar environments and exploration to represent movements in novel environments (Réale et al. 2007). Invasion-front mynas had larger exploratory home ranges, moved greater maximum distances each day, and changed overnight roost locations more often than their counterparts from long-established sites, suggesting that our prediction of higher exploration in front mynas was upheld. We also found that, although mynas at the invasion front did not move more often than mynas at long-established sites (as measured by probability of moving), their movements when they did move were larger (as measured by mean distance moved per move), suggesting that front mynas were also more active, as predicted. Exploratory home ranges were ~ 21 times larger than core home ranges on the invasion front, but only ~ 9 times larger at the invasion source. These stark behavioral differences were present over and above variation attributable to environmental conditions, namely rainfall and temperature. To the best of our knowledge, this is the first empirical study to show invasion-stage, population differences in dispersal-relevant behavior in an invasive bird under free-ranging conditions. The pattern is in line with higher exploration found in invasion front house sparrows and cane toads in captive tests (Liebl and Martin 2012; Gruber et al. 2017).

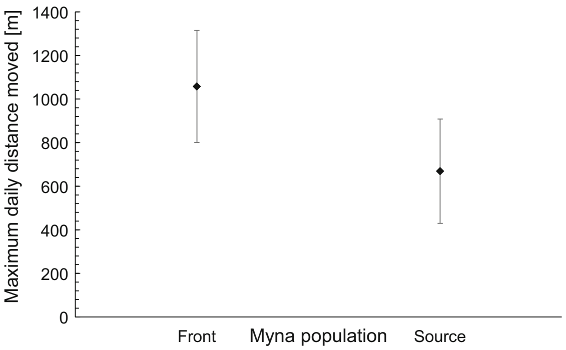

Fig. 5 Exploratory behavior (Maximum daily distance moved (mean ± 95% CI)) of common mynas in recently-established, invasion front and long-established, source populations. Depicted means represent marginal means from MAMS (Tables 1 and 2)

Inter-individual variation in activity and exploration are viewed as a personality syndrome (Cote et al. 2010b), which predicts dispersal tendency in a diverse range of taxa (Dingemanse et al. 2003; Alford et al. 2009; Cote et al. 2010b; Quinn et al. 2011; Thorlacius et al. 2015). Therefore, the finding that front mynas are more exploratory and more active provides support for a model by which mynas range-expand by spatially sorting according to inter-individual variation in dispersal-relevant traits. Evidence for such a model first arose from a study of the South African myna range expansion. Mynas were introduced by humans to South Africa in 1902 and 1938 and, similar to Australian mynas, are currently spreading (Berthouly-Salazar et al. 2012). Studying a sample of nearly 400 mynas, Berthouly-Salazar et al. (2012) showed that wing length and wing ratios (residuals from the regression of wing length against body size) increase in female (i.e. the dispersing sex), but not male, mynas with distance from the point of introduction. Further, variation in female wing morphology was not predicted by bioclimatic variation, nor variation in vegetation cover, contrary to variation in bill ratio (residuals from the regression of bill length against bill width) (Berthouly-Salazar et al. 2012). Similarly, in the present study neither temperature, nor rainfall had a significant effect on any of our measures of exploration or activity, suggesting that heightened exploration and activity are not a function of local climatic differences (Berthouly-Salazar et al. 2012). The difference in a dispersal-relevant behavioral trait between invasion front and source mynas found here, coupled with the geographical cline in a dispersal-relevant morphological trait in South Africa yield convergent evidence for a model of spread in which mynas spatially segregate according to inter-individual variation in dispersal tendency (Alford et al. 2009).

Invasion stage is not, however, the only possible explanation for front-source differences in behavior found here. Environmental variation, including availability of preferred habitat and its spatial configuration, is known to exert a strong influence on movement behavior (Melbourne et al. 2007; Real et al. 2016). For example, daily and seasonal patterns of feral pigeon (*Columba livia domestica*) movements are strongly affected by resource distribution and availability (Soldatini et al. 2006), and exploratory behavior is state-dependent in Eurasian tree sparrows (*Passer montanus*), with hungry individuals showing more exploratory behavior (Lee et al. 2016). In order to increase the likelihood that any differences in behavior were attributable to invasion stage rather than environmental variation between front and source locations, we matched the habitat of all selected trapping sites as closely as possible using satellite imagery, and sampled mynas from two front and two source replicate populations. Matching habitat was more feasible at a local spatial scale (< 1 km^2) (Fig. 1), but less so at a broader spatial scale (> 4 km^2) (Fig. 2). This is due to the westward range expansion of mynas from coastal (large) to inland (smaller, more rural) towns. Trapping sites on the myna invasion front were necessarily in small townships where urban habitat subsides more quickly to rural land, whereas trapping sites in long-established areas were in larger coastal cities (Figs. 1, 2). Despite similar urban densities at the local scale, the spatial distribution (e.g., clumped versus dispersed) of habitat resources such as food, water, and roosting locations might have differed between the front and source townships despite our efforts to match them, which might have caused the birds to behave differently. Indeed, prior research has shown that movement behavior can vary even among cities. For example, in some cities, a majority of feral pigeons, like their wild rock dove ancestors (*Columba livia*), fly to adjacent agricultural areas to feed, whereas in other cities, no such flights are recorded (Rose et al. 2006 and references therein).

Although we cannot completely rule out that the front-source differences in exploration and activity found here were habitat-induced rather than related to invasion stage, we provide a few arguments against this interpretation. Prior research has shown consistently that mynas are overwhelmingly found in urban environments (Crisp and Lilli 2006; Shanahan 2012; Sol et al. 2012; Haythorpe et al. 2014; Old et al. 2014), have small home range sizes (0.1 km^2, Kang 1989, 1992), travel relatively small distances compared with other birds species (Kang 1992; Berthouly-Salazar et al. 2012), and are considered sedentary based on genetic analyses (Ewart et al. 2018). Together, these patterns make it less likely that front mynas, like feral pigeons in some cities, were routinely travelling to adjacent agricultural areas to feed. This is further supported by the fact that our measure of exploration captured rare long-distance excursions meaning that these journeys did not reflect regular feeding habits, unlike urban populations of feral pigeons (Rose et al. 2006). Furthermore, prior research has found that rural mynas are significantly larger than urban mynas (Old et al. 2014). In rural areas, mynas can achieve weights of > 130 g, whereas urban mynas were < 115 g (Old et al. 2014). This size difference was attributed to higher quality food (e.g., arthropods) in rural than urban environments (Old et al. 2014). Given that prior research has demonstrated that hunger increases exploration (Lee et al. 2016), the argument that front sites might be more 'rural' would generate a prediction of reduced exploration rather than increased exploration. Therefore, we suggest that the direction of the differences observed here (front mynas are more exploratory) is inconsistent with a model of invasion in which dispersal is random relative to phenotype and settlement in new areas is followed by local adaptation. Finally, mynas from both front and source locations were well within the size range of urban, rather than rural, individuals based on previous work (front: 109.0 g ± 9.4 g; source: 108.5 g ± 8.3 g) (Old et al. 2014), making it unlikely that they routinely used rural areas surrounding the front townships to forage (Fig. 2) as one might expect from rural-based birds (Old et al. 2014).

To be relevant to invasion, intra-species variation in morphology and behavior both need to enhance dispersal. For morphology, this relationship has been established in insects due to the existence of dispersal morphs that display distinct wing morphologies and differ in their dispersal capacities (Harrison 1980), in toads by measuring movement distances and leg length jointly (Phillips et al. 2006), and in birds by relating wing morphology to variation in flight biomechanics (Pennycuick 2008). For behavior, more specifically exploration and activity as these traits are relevant to the present study, a positive association with dispersal tendency has been shown in a range of mammals, birds, and fish, as well as invertebrates (Dingemanse et al. 2003; Krackow 2003; Hoset et al. 2011; Quinn et al. 2011; Knop et al. 2013; van Overveld et al. 2014; Thorlacius et al. 2015; see also for a review: Wey et al. 2015). Not only is exploration consistent across time and contexts in several bird species (Verbeek et al. 1994; Guillette et al. 2015), including common mynas (Lermite et al. 2017; Perals et al. 2017), exploration is also heritable in fish (Dingemanse et al. 2009), mammals (Careau et al. 2011; Kanda et al. 2012) and birds (Dingemanse et al. 2002; Quinn et al. 2009; Korsten et al. 2010) and shares a genetic underpinning with dispersal in great tits (*Parus major*) (Korsten et al. 2013). Overall, this body of work supports the idea that inter-individual variation in exploration behavior could create targets of selection, and therefore consistent inter-individual variation relevant to the spread of this alien bird (Berthouly-Salazar et al. 2012).

In their study of Southern African mynas, Berthouly-Salazar et al. (2012) found that the cline in wing length was only present in females and not in males. The female-specific nature of the morphological change strongly favors a spatial sorting model of spread given that females are likely to be the dispersing sex as is the case in most socially monogamous sedentary bird species (Berndt and Sternberg 1968; Baker 1978; Greenwood 1980; Greenwood and Harvey 1982). While the present study did reveal some effects of sex on non-breeding season exploration and activity behavior, a time of year at which mynas are congregating at communal roosts, these did not show a consistent pattern and effect sizes for sex were always smaller than those for invasion stage. For example, although there was a tendency for female mynas to be more exploratory on both the invasion front and the invasion source (as measured by larger daily maximum distances moved), as might be expected if females are prospecting potential future territories, this sex effect was non-significant. Although core home range size was influenced by sex, males had larger core home ranges than females at the source but smaller ones on the invasion front. Currently, we do not know why source male mynas have larger home ranges. Understanding the mechanisms and timing of mate choice and territory prospecting and establishment might help elucidate this invasion stage difference.

We also found that activity varied with conspecific density in opposite directions across the two stages of the invasion: activity increased with increasing conspecific density in the source, but decreased with increasing population density in front populations. Perhaps as populations increase in long-established populations, birds need to travel further to find available territories. In contrast, in recently-established populations, increasing population densities select for local aggregation. More research is needed to better understand how myna behavior changes as a function of population density as has been undertaken in bluebirds (Duckworth and Badyaev 2007).

In conclusion, our study shows that common mynas from invasion-front populations were significantly more exploratory and more active than common mynas from long-established populations. This is the first study to use wild, free-ranging birds to show increased exploration and activity at an invasion front, and results are in line with research showing that invasion-front house sparrows in North America (Liebl and Martin 2012) and cane toads in Northern Australia (Alford et al. 2009; Gruber et al. 2017) are also more exploratory. The differences in exploration and activity were better explained by differences in invasion stage than variation in conspecific density or by sex, and were not explained by variation in temperature and rainfall. These behavioral differences are consistent with spatial selection theory (Phillips et al. 2008, 2010; Lee 2011; Shine et al. 2011a, b), as well as previous findings from mynas on the South African range expansion. Nevertheless, alternative tests of this model are needed to elucidate further the relative role of selection neutral versus adaptive processes in the range expansion of Australian common mynas. One possible approach would be to translocate front mynas to source locations and vice versa and to radio-track the birds following release. If, after translocation, the invasion-front birds maintained their high exploration and activity levels and the long-established birds maintained their low exploration and activity levels, this would suggest that exploration and activity behaviors are an individual attribute rather than induced by the immediate demands of the local environment. Alternatively, a common garden approach in which birds from front and source populations are reared under identical conditions might be feasible in this species (Miranda et al. 2013). Elucidating the relative roles of spatial sorting versus local adaptation will contribute to developing more realistic models of range expansion that integrate inter-individual trait variation and evolutionary processes (Clobert et al. 2009; Ramanantoanina et al. 2014; Weiss-Lehman et al. 2017; Cote et al. 2017).

Acknowledgements We thank Thomas Gaffney for assistance in the field. The research was supported by a Commonwealth Australian Research Council Discovery Project 2014 to SK and ASG.

Author contributions JB, ASG and SC conceived and designed the study. JB conducted the field work. JB, KC, SC and ASG analysed the data. SK contributed to the development and implementation of the front/source components of the research. All authors contributed to preparing and editing the manuscript.

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