Biol Invasions
https://doi.org/10.1007/s10530-018-1798-9

ORIGINAL PAPER

Investigating responses to control: a comparison of common myna behaviour across areas of high and low trapping pressure

Marie C. Diquelou · Geoff R. MacFarlane · Andrea S. Griffin

Received: 10 October 2017 / Accepted: 17 July 2018

Abstract Harvesting of wildlife by humans is commonly known to impact target species' demography, life history and behaviour. Yet in the context of invasive and pest species control, behavioural shifts have received very little attention. The introduced common myna, *Acridotheres tristis*, is undergoing intensive control efforts in some areas of its Australian distribution. In order to investigate whether myna populations respond to harvesting, we compared the behaviour of free-ranging common mynas in areas of high and low trapping pressure. Behavioural analyses revealed that mynas in high trapping risk areas stayed closer to refuges, tended to form smaller groups, and were overall less detectable. Behavioural differences between high and lowly trapped areas were not attributable to variation in population density. Overall, these results are consistent with the hypothesis that common mynas have the potential to adjust their behaviour in response to heightened anthropic risk in the environment. Behavioural shifts in invasive alien species could modify their ecological impact and may interfere not only with the effectiveness of control measures, but also with how their effectiveness is assessed. Future research should aim to isolate behavioural mechanisms underpinning compensatory responses to control so that any potential effects can be mitigated.

Keywords Wildlife harvesting · Invasive species · Detectability · Wildlife management

Introduction

Whether in the context of consumption, recreation, science, or control, humans often collect individuals from populations of wild animals. This wildlife harvesting has the potential to elicit changes in a large range of traits of the target species. For example, fishing and hunting have been shown to shape the morphology and life-history of targeted species (Coltman et al. 2003; Kuparinen and Merilä 2007; Fenberg and Roy 2008; Pigeon et al. 2016; Sullivan et al. 2017). Wildlife harvesting can also influence the behaviour of prey. In many species, prey populations become more risk averse during periods of high human predation (Arlinghaus et al. 2016). For instance, brown bears (*Ursus arctos*) change their activity patterns to be more nocturnal during the hunting season (Ordiz et al. 2012), and some fish species are more avoidant of fishing gear in areas that support a high pressure of recreational angling (Alós

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-018-1798-9) contains supplementary material, which is available to authorized users.

M. C. Diquelou (✉) · G. R. MacFarlane · A. S. Griffin
University of Newcastle, Callaghan, NSW 2308, Australia
e-mail: Marie.Diquelou@uon.edu.au

et al. 2014). Such behavioural adjustments may be a result of evolutionary processes, whereby harvesting systematically selects animals on heritable behavioural traits (e.g. boldness), or may result from processes related to phenotypic plasticity, such as learning. While the mechanisms responsible for these changes remain poorly understood, some species have clearly been shown to adjust their behaviour in ways that reduce the likelihood of human harvesting.

The capacity of targeted species to reduce human harvesting risk has far reaching implications for management of alien and pest species. While theoretical and applied research in this field has typically adopted a demographic focus, behavioral effects have recently emerged as a key consideration (Côté et al. 2014; Le Saout et al. 2014). Because eradication is seldom achievable outside of islands, alien and pest populations are often managed over the long-term, leaving considerable evolutionary and ontogenetic time for behavioural changes to arise. Beyond the possibility that behavioural change might reduce the effectiveness of species management, there is also scope for these changes to modify, for better or for worse, the species' ecological impact(s). The case of lionfish (*Pterois volitans*) is particularly telling: populations undergoing culling efforts modify their behaviour as well are their temporal and spatial distribution in such that a way that, not only are they less susceptible to control, they may also threaten more native species (Côté et al. 2014). Quantifying population behavioural change in targeted pest species is of paramount importance to strategic planning and management.

Equipment used for wildlife harvesting and species management do not resemble prey species' natural predators in either morphology or behaviour. This is particularly true for passive techniques (e.g. trapping, recreational fishing), which have few equivalents in the natural world outside, perhaps, of arthropod trap-like structures and certain sit-and-wait predators. Hence to recognize harvesting equipment as presenting a threat, most animals will not be able to rely on "archetype recognition" and "recoverable templates", but may instead need to rely on mechanisms that allow for rapid change such as learning, phenotypic plasticity and rapid evolution (Carthey and Blumstein 2018).

Regardless of the mechanism behind the development of equipment recognition per se, we argue based on the literature on responses to human harvesting, some of which we have outlined above, that the presence of novel anthropic threats in the environment is likely to affect the target species' perceived level of environmental risk and to alter its behaviour (Lima and Dill 1990). This is particularly so for those threats that are associated with a rich array of acoustic and visual stimuli that are, contrary to the equipment per se, likely to be recognized evolutionarily and ontogenetically as threat-relevant cues, such as dead or fearful conspecifics, and alarm signals.

The common myna (*Acridotheres tristis*) is a highly successful invader (Lowe et al. 2000; Peacock et al. 2007). In Australia, following evidence that they compete with native secondary cavity-nesting species (Pell and Tidemann 1997; Grarock et al. 2012), mynas have become the target of significant trap-and-cull efforts in some areas of their distribution. In the light of numerous anecdotal reports of emerging trap shyness, as well as a small-scale analysis indicating that abundances remain stable while trapping success declines in heavily trapped Canberra suburbs (King 2010), we undertook a large-scale comparative study of risk-taking behaviour in mynas.

The aim of this study was to investigate whether mynas show population-level changes in behaviour in the presence of harvesting. In doing so, we assumed that mynas are capable of perceiving and responding to a novel anthropic threat in their environment. Even though walk-in baited traps (the most widely used trap in Australia) per se lack morphological and behavioural similarity with mynas' natural predators (e.g. hawks, cats), trapping activities, particularly when humans interact with trapped birds, are often accompanied by a rich array of threat-relevant cues to which mynas respond to, and learn from, including fearful conspecifics and alarm calls. For example, we have previously shown that pairing of humans and conspecific fear responses triggers place avoidance learning in mynas (Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). We have also shown that mynas become more wary of objects associated with conspecific alarm calls (Griffin 2008, 2009). Hence, we argue that it is reasonable to assume that mynas have some capacity to perceive environments where they encounter trapping activities as more risky.

After locating zones in which mynas were undergoing different trapping pressures, we compared a range of behavioral variables between highly and lowly harvested areas. The literature on animal responses to trapping is scarce. Hence, rather than drawing upon intuitions to speculate which behaviours might change, and therefore which behaviours should be measured, we developed predictions based on studies of prey responses to risk available in the wildlife-harvesting and the large, classical anti-predator literatures. While traps are very different from mynas' historical and current predators, the anti-predator literature is the richest available source of information about how animals respond to increased threat levels. Additionally, it is less parsimonious to predict that completely new responses will emerge when faced with a novel threat; rather, existing responses, those that have been shaped by natural predators, are likely to be generalized to new contexts, particularly when those contexts contain familiar threat-relevant cues, such as dead and fearful conspecifics (Griffin et al. 2000, 2001). It is important to note that we make no assumption as to whether any of the predicted behavioural changes are adaptive in the face of trapping, as this will depend upon the mechanism by which the changes arise, and the time course of change. These were not aspects our study was designed to investigate (see "Discussion" section).

First, we predicted changes to several generalized risk-relevant behaviours. We predicted that mynas in risky areas would form larger groups as expected from the collective detection and risk-dilution hypotheses (Krause and Ruxton 2002). We also predicted that mynas in risky areas would become less detectable (King 2010; Côté et al. 2014) and spend less time foraging away from refuges (Slotow and Coumi 2000; Caro 2005). Second, we predicted several behavioural changes more specific to the present threat. We expected mynas in heavily trapped areas to be less active, a behaviour that has been suggested to reduce chances of encounter with passive capture devices (Alós et al. 2012). We also expected these mynas to be more responsive to conspecific distress calls (Griffin 2008). Abundance was estimated in each sampled area to determine to what extent differences in population density might explain the observed differences in behaviour.

Materials and methods

Sampling strategy

Behavioural sampling of myna populations was undertaken from June 2012 to October 2012 in the coastal "larger Sydney" region in New South Wales (NSW) and in the inland "larger Canberra" region in the Australian Capital Territory (ACT), in Australia (Appendix 1.1 of Electronic Supplementary Material).

Trapping pressure estimates were drawn from a prior survey of trapping activities in local administrative units (i.e. *localities*) across the entire NSW and ACT distribution of the common myna (Appendix 1.2). The returned questionnaires provided data on the number of common mynas captured per year of trapping activity, which was then divided by the number of units of 1000 inhabitants (a unit we will refer to as khab from hereon after) in the locality to obtain a trapping pressure index (Appendix 1.3). Considering this index was based on self-reported levels of trapping activity, we allocated them to coarse categories in order to account for potential uncertainty and error: a threshold of 10 mynas per year per khab was determined as a cut-off point between low and high trapping pressure.

Four localities with high trapping pressure and five localities with low trapping pressure were selected across both regions. Within each locality, several sampling areas (SAs) of 2 × 2 km were placed in such a way that their surface was covered mostly by suburban habitat and contained no more than 15% of bushland and parkland in total. The number of SAs in a locality depended on its surface, with more SAs in larger localities (mean 3.5, range 2–5). A total of 32 SAs were sampled in this study, 15 in high trapping pressure localities and 17 within low trapping pressure localities (Appendix 1.4).

Point-count and transect methodology

We undertook surveys to estimate common myna abundance in each SA. We chose to perform point-counts as to better account for potential variation in conspicuousness (Bibby et al. 1998). Eight point counts took place in each SA: one was arbitrarily set in commercial habitat (in which mynas often congregate), and the seven other locations were randomly selected. Point-counts plots consisted of 50-m radius areas and were always separated by a distance of at least 300 m. The surveys were conducted during the 3-h period prior to sunset, and lasted 5 min. All birds seen within or beyond the 50-m plot edge, were recorded except those flying high overhead. If any doubt as to whether a bird had already been counted, it was excluded.

Distance to the experimenter was measured by locating birds on maps marked with five concentric circles of 10, 20, 30, 40 and 50 m radii. Birds outside of the 50-m boundary were noted as "beyond 50 m". For the purpose of the analysis, an arbitrary maximum distance of 100 m at which birds could be seen was selected. Observers remained in the 10-m central zone during the entire duration of the point-count.

In addition to point-counts, transects were undertaken. In each SA, within 4 h from sunrise, on the morning after the point-counts took place, the observers walked through the SA at a constant slow pace, looking for mynas without following a predefined path. The main goal of these transects was to sight as many mynas as possible so that their behaviour could be sampled. Hence, transect path and location were selected based on daily information collected during and in-between point-counts and with the goal of maximizing the likelihood of encountering mynas.

The path walked during each transect was recorded on a map in order to measure the distance walked. All mynas sighted within 25 m from the observers were recorded, creating a 50 m-wide transect. The combination of transect width and length allowed the surface surveyed to be calculated (average surface surveyed per SA 37 ha ± 1.20SE, approximately 9% of the total SA surface). The observers never walked twice in the same place and recorded all mynas sighted in a way that minimized the number of birds that were counted twice.

For each point-count plot, the percentage covered by each of three land use categories (parkland, residential, urban, see Appendix 1.5) was determined by eye from satellite images (Google Earth$^{\mathrm{TM}}$). The category that covered the greatest proportion of the plot area was used to characterize its habitat.

Temperature was recorded once at the beginning of every point-count and every hour during transects. Surveys were only carried out in clement weather, avoiding high winds and rain. The 5-month period over which the fieldwork was conducted was divided into two seasons: winter (June–August) and spring (September–October). Overall this distinction corresponds to the non-breeding (winter) and the beginning of the breeding season (spring) of mynas.

Behavioral observations

General behaviour

All mynas sighted, whether individually or in groups, whether during point-counts or transects, were counted as an 'observation'. These observations were considered to be independent because the sampling strategy reduced the likelihood of repeated sampling of individuals. For each observation, we noted:

- the size of the group (number of mynas within 10 m of each other during at least 30 s),
- whether the group was close to a refuge (i.e. if the center of the group was less than 2 m away from either a perching point or cover),
- and its activity (five mutually exclusive categories: calling, foraging, walking, flying, standing still).

Responsiveness to social signals of predation risk

Responsiveness to social risk signals was assessed by measuring the mynas' responses to distress call playbacks. Distress calls are high amplitude, broadband vocalizations that are produced by small birds in response to seizure by a predator, including humans and are indicative of high predation risk (Conover 1994). Under free-ranging conditions, common mynas respond to distress call playbacks by approaching the source of the sound (Griffin 2008).

Each playback was flanked by two 5-min point-counts (see procedure above). Specifically, once an initial 5-min point-count period was over (pre-playback survey), the observers initiated a second point-count from the same position (post-playback survey). The post-playback survey followed exactly the same protocol as the pre-playback survey except that it began with a 1-min distress call playback (Appendix 1.6) and observers noted whether the groups of mynas present responded to the playback. Responses were defined as any abrupt change in activity following the onset of the playback. The function of this type of call is open for debate (Conover 1994). Therefore, we included different behaviours as responses (i.e.

approaching the speaker, flying to a high perching point and freezing). As long as one individual in the group responded, the group was considered to have responded to the playback. Myna responses were recorded as soon as the 1-min playback began and for 4 min after it ended. In this way, pre-playback and post-playback surveys had the same duration.

Detectability

Non-random selection of transects in order to maximize the number of mynas encountered had for consequence that we expected abundance estimates based on transects to be greater than those obtained from point-counts. However, we predicted that this level of inflation would vary across SAs as a function of the trapping pressure experienced by birds. Indeed, Bibby and co-authors (1998) state that point-counts are more likely to lead to the detection of cryptic birds, while transects on the other hand, are, more likely to lead to more sightings simply due to sampling a larger area, making them better suited to counting conspicuous birds. These considerations suggest that if our transects led to an inflation of myna densities compared to point-counts, then this inflation should be more important where birds were most conspicuous. Based on the hypothesis that trapping pressure causes mynas to become shier, we made the following prediction: in low trapping pressure SAs, where birds should be conspicuous, transect density estimates were expected to be much higher than those obtained from point-counts. In contrast, in high trapping pressure SAs, where mynas should be more discreet, we expected abundance estimates based on transects to be only slightly higher than those based on point-counts.

In addition to conspicuousness, rarity of birds was also expected to influence differences between transect and point-count density estimates. This is because transects allow to search larger surfaces, so birds that at very low density (i.e. rare) are more likely to be encountered during transects than point-counts. Overall, we expected the difference between transect and point count density estimates to be a function of an interaction between trapping pressure and myna density. Predictions regarding the extent to which we expected transects to inflate density estimates in comparison to point-counts under different trapping pressure and density scenarios are summarized in Table 1.

Table 1 Predicted tendency of transects to inflate density estimates relative to that found in point-counts, depending on trapping pressure and relative density of common mynas

Trapping pressure	Low	High
Expected myna behaviour	Conspicuous	Discreet
High density (birds are common)	Moderate	Low[b]
Low density (birds are rare)	High[a]	Moderate

[a] Predicted high inflation index indicates that density estimates produced by transect surveys are expected to be much higher than those produced by point-counts. This is expected to occur when mynas are at low density and when they are conspicuous (when trapping is risk is low)

[b] On the other hand, when mynas are discreet (as is expected under high trapping pressure) and when they are at high density, then, transects are expected to produce density estimates that are only slightly higher than estimates from point-counts (i.e. low inflation)

Another approach to investigating differences in detectability is to estimate the likelihood of seeing birds in places where their presence can be established with certainty. We took advantage of the fact that common mynas are very vocal throughout the year (Feare and Craig 1999) to ascertain that they were present in the vicinity of a point-count plot. This then allowed us to investigate the factors underpinning the likelihood of visually detecting mynas in plots where mynas had been detected acoustically and were therefore known to be present. Mynas were heard in 97 out of 227 point-counts surveys (43%), while only seen in 20% of plots. Auditory detections were hence much more common than visual detections, which validates the approach taken here, especially since they were extremely few cases (n = 3) where mynas were seen in plots in which they were not heard.

Analysis

Abundance estimates

In the present study, transects were performed in the morning and point-counts in the afternoon. In analyses that used abundance data from point-counts, time of day was defined as “time to sunset”, where zero was set at sunset. In analyses that used data from both point-counts and transects, we expected time from the closest period of dark to be the most relevant biological influence on myna behaviour. Mynas form communal roosts during the night and periods with large aggregations and high activity are often seen before and after roosting. Hence, we defined "time-to-dark", which referred to *time from sunrise* in the morning (zero set at sunrise), and *time to sunset* in the afternoon (zero set at sunset).

Number of birds detected at each of the 253 point-count plots was used to estimate abundance. We used a zero-inflated model to account for the high proportion of plots in which no birds were seen (80%). The negative-binomial distribution was chosen over the Poisson distribution because over-dispersion was present over and above the zero-inflation. Zero-inflated negative binomial GLMMs were fitted with the R package glmmADMB package (Fournier et al. 2012). The initial model included trapping pressure, region, the interaction of trapping pressure and region, habitat, season, temperature and time to sunset. Non-significant predictors were removed successively until only significant predictors were left in order to obtain a minimum adequate model (MAM). Because trapping pressure was the key variable of interest in the present work, it was always retained in the model regardless of whether it was a significant predictor or not. We then verified that this model was an improvement over simpler and more complex models using likelihood ratio statistic (Zuur et al. 2009).

The fully nested random-intercept structure of the data collection (region/locality/SA) could not be used because region had too few levels to be incorporated as a random variable (N = 2). The (locality/SA) nested structure elicited model failures when entered into the model alongside the zero-inflation. For these reasons, only locality was included as a random factor. It is worth noting that SA explained very little of the variance of the minimum adequate model without zero-inflation (locality:SA variance = $2.33 \times 10^{-9} \pm 4.83 \times 10^{-5}$) and that the MAM revealed the same significant predictors whether zero-inflation was accounted for or not.

Detectability analysis

In each of the 32 SAs, 8 point-count surveys took place. By considering only birds within the 50-m point-count plot boundary, we calculated a density estimate that could be compared to that obtained from transects. To evaluate to what extent transects inflated density estimates found in point-counts, we calculated an inflation index by extracting residuals from a linear regression of the two density estimates (Appendix 1.7.a). In order to account for rarity, SAs with an average point-count density of 0.5 mynas per hectare or below were categorized as "low density", while those with higher densities were categorized as "high density". We tested whether the inflation indexes differed by using an ANOVA including trapping pressure and rarity as factors.

In order to compare visual and auditory detections, we used only data from the initial (pre-playback) point-counts. The subset of 97 plots where mynas were heard was used to investigate the likelihood of seeing mynas when mynas were heard. The likelihood of seeing at least one myna was modeled using a binomial GLMM with the lme4 package (Bates et al. 2015) with a nested random-intercept structure (Locality/SA). Model selection was done through a stepwise backward procedure for which the initial model contained the following terms: trapping pressure, region, the interaction of trapping pressure and region, habitat, season, temperature and time to sunset. Once again, trapping pressure was retained in the model throughout the backward elimination process as it constituted a key variable of interest.

General behaviour

To model the effects of trapping pressure on behaviour, we used a stepwise backward model selection procedure, retaining the key variable of interest, namely trapping pressure, throughout the process. Other predictor variables included in the initial full-model were: region, the interaction of trapping pressure and region, survey type, season, time to dark and abundance, as well a nested random-intercept effect (locality/SA). Temperature caused collinearity issues with season, region and survey type, and hence could not be included as a factor in the full model. The abundance estimate used in these models was calculated by averaging the number of birds seen inside each point-count plot across that SA.

Group size was analyzed using a zero-truncated negative binomial GLMM with the glmmADMB package (Fournier et al. 2012). Likelihood of birds being close to a refuge was analyzed by fitting a binomial GLMM (LME4 package). Activity was analyzed using a multinomial log-linear model with the five activity categories as the outcome variable with the "standing still" category as the reference category. This was done with the nnet package (Venables and Ripley 2002) following the method suggested by Agresti (2002). The initial model contained all factors listed above except the interaction term. A follow-up Wald test was then performed to identify more precisely which activities were affected by the significant factors.

Responsiveness to social signals of predation risk

Comparison of the number of birds seen during point-counts before and after the playback was undertaken following the same methodology as described for abundance. The data from the pre-playback and post-playback point-counts were combined such that each plot had two counts which required the addition of a random factor to account for repeated measures on the same point-count plot. The full random structure (locality/SA/plot) was used in this model. A variable called "stage" which referred to whether the count took place before or after the playback was added to investigate whether the playback significantly influenced the number of birds seen.

The likelihood of myna groups responding to distress call playbacks was analyzed using a binomial GLMM. The initial model included trapping pressure, region, the interaction of trapping pressure and region, time to sunset, temperature, distance to the experimenter (median of distance bin) and group size. The nested random-intercept structure (locality/SA) was included.

All analyses were undertaken using R version 3.2.2 (R Core Team 2015).

Ethical statement

All work was approved by a New South Wales National Parks scientific license #12304 and an Australian Capital Territory animal use research license granted to Andrea Griffin in September 2011. In addition, all protocols were approved by the University of Newcastle Animal Ethics Committee (protocol #A-2011-129).

Results

Abundance

Point-count surveys were performed in the afternoon, and the number of mynas detected increased as sunset approached which may reflect the tendency of mynas to congregate before roosting for the night (Table 2). More birds were seen in the Sydney region (mean = 1.23 ± 0.26SE birds per plot) than in the Canberra region (mean = 0.41 ± 0.10SE birds per plot) and less birds were seen in highly modified urban habitats than residential ones (Table 2). Trapping pressure of localities did not predict abundance (Table 2).

Table 2 Parameter estimates from minimal adequate zero-inflated negative binomial mixed model of the number of mynas seen per point-count

Fixed coefficients	Estimate	SE	z-value	*p*
(Intercept)	1.383	0.450	3.075	0.002
Trapping pressure (low)[a]	0.381	0.301	1.267	0.205
Region (Sydney)[a]	0.590	0.292	2.017	0.044
Habitat (Park)[a]	− 0.649	0.482	− 1.346	0.178
Habitat (Urban)[a]	− 0.794	0.383	− 2.071	0.038
Time to sunset	− 0.584	0.175	− 3.330	0.001
Random effects	**Variance**	**SD**		
Locality	2.061×10^{-9}	2.219×10^{-8}		

[a] Categorical variables in the table are compared to a reference category, region: Canberra, trapping pressure: high, habitat: residential. When a variable contains more than two categories, all are compared to the same reference category

Detectability

Density estimates from point-counts and transects were significantly but not highly correlated (Pearson's r = 0.51, $p = 0.03$). In line with our predictions, we found that transects had higher estimates (mean = 1.27 ± 0.19SE bird per ha) than point-counts (mean = 0.66 ± 0.12SE bird per ha) (ANOVA, F(1,62) = 7.52, $p = 0.008$). We found that low trapping pressure areas tended to have larger inflation indexes than high trapping pressure areas (Appendix 1.7.b). This difference fell just short of significance, however (two-way ANOVA, F(1,29) = 3.71, $p = 0.064$). Based on the assumption that transects have a reduced tendency to inflate density estimates relative to point-counts in areas where mynas are discreet, this result suggests that there is a trend for mynas in high trapping areas to be less conspicuous than their conspecifics living in low trapping areas. Although it was expected that transects would allow observers to see more birds in areas with low densities, this was not supported by the data: high and low density areas did not differ in their inflation indexes (two-way ANOVA, F(1,29) = 1.12, $p = 0.299$).

Trapping pressure was not a significant predictor of the likelihood of seeing mynas in plots where they were heard (binomial GLMM, $\text{estimate}_{\text{low.pressure-}} = 0.577 \pm 0.463\text{SE}$, $p = 0.212$, see Appendix 2.1). However, the likelihood of detecting mynas visually in plots where mynas were heard was higher in the Sydney region than in the Canberra region (binomial GLMM, $\text{estimate}_{\text{sydney}} = 1.352 \pm 0.438\text{SE}$, $p = 0.002$). This indicates either that mynas in these two regions differ in their behaviour such that they are more likely to be seen in Sydney than in Canberra, or alternatively that the two regions differ in some aspect that makes mynas easier to see in Sydney than in Canberra.

Behavioral observations

The number of individuals within groups varied substantially (mean 1.86, range 1–18) over the 914 observations that were made during this study. However, the majority of groups consisted of one or two individuals (n = 794, 87%). Group size was on average smaller in spring than in winter (Table 3, Fig. 1) and observations of larger groups were made more often at times closer to dark (early in the morning and late in the evening). There was also a strong trend for smaller groups under high trapping pressure (Table 3).

In accordance with our predictions, tendency to be close to a refuge was higher in areas under high trapping pressure, and this was particularly true in Canberra as suggested by the significant interaction (Table 4).

Of all five possible activities, standing still was the most common activity category recorded (N = 301/891). When determining which factors predicted the probability of mynas of engaging in an alternative activity to standing still, group size, region, season and trapping pressure remained in the minimum model while survey type, abundance and time to dark did not. Predictors of whether mynas were more likely to be observed moving, vocalizing, foraging or flying than standing (baseline category) are indicated in Table 5. In line with a large literature on group size effects on

Table 3 Parameter estimates from minimum adequate zero-truncated negative-binomial mixed model on the number of individuals in a group

Fixed effects	Estimate	SE	z-value	p
(Intercept)	− 0.543	0.206	− 2.638	0.008
Trapping pressure (low)[a]	0.322	0.165	1.950	0.051
Season (winter)[a]	0.588	0.158	3.722	< 0.001
Time to dark	− 0.159	0.063	− 2.537	0.011
Random effects	**Variance**	**SD**		
Locality:SA	0.083	0.288		
Locality	8.66×10^{-9}	9.31×10^{-5}		

[a] Categorical variables are compared to reference category which is not indicated above. Trapping pressure: high, season: spring

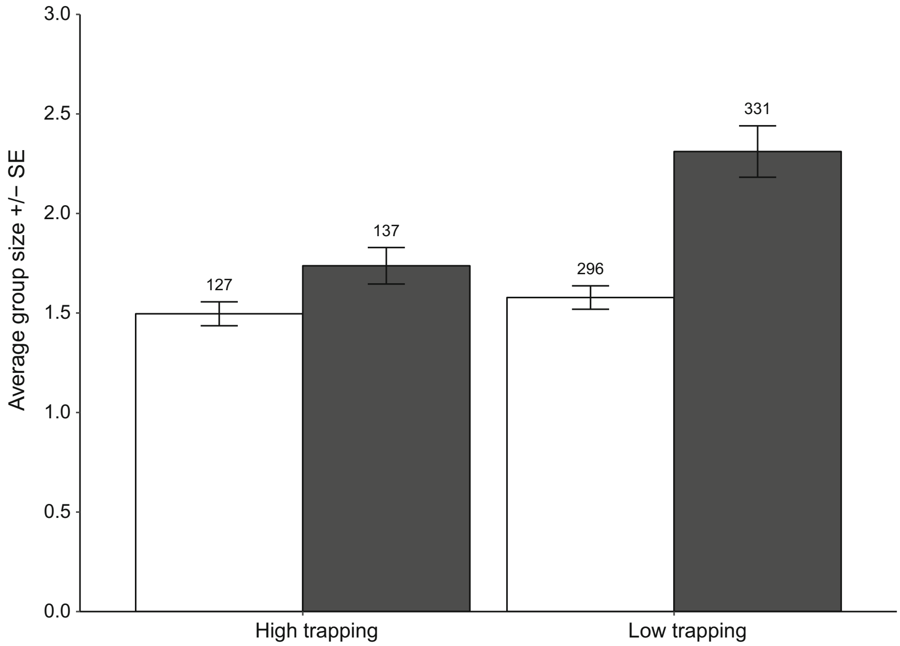

Fig. 1 Mean group size observed among mynas in high and low trapping pressure environments as a function of season, with spring in white and winter in dark grey. Numbers above bars indicate sample size

Table 4 Parameter estimates from minimum adequate binomial mixed model on the likelihood of mynas of being close to a refuge. A bird was considered close to a refuge when it was less than 2 m away from either a perching point (at least 2 m-high), or cover (such as a dense bush)

Fixed effects	Estimate	SE	z-value	p
(Intercept)	1.660	0.227	7.299	< 0.001
Trapping pressure (low)	− 0.816	0.279	− 2.925	0.003
Region (Sydney)[a]	− 0.773	0.303	− 2.547	0.011
Trapping pressure: region	0.758	0.359	2.112	0.035
Random effects	**Variance**	**SD**		
Locality:SA	3.88×10^{-15}	6.23×10^{-8}		
Locality	0.00	0.00		

[a] Categorical variables are compared to reference category which is not indicated above. Region: Canberra, trapping pressure: high

foraging, mynas in larger groups were significantly more likely to be observed foraging relative to standing still (Table 5). Moreover, vocalizations were less common during winter, outside the breeding season (Table 5). Trapping pressure influenced activity of mynas such that mynas were significantly less likely to be engaging in locomotion under low rather than high trapping pressure (Table 5).

Response to distress calls

While the sound of myna distress calls increased the number of mynas detected (see Table 3 of Appendix 2.2), stage was not a significant predictor of the number of birds seen (negative binomial GLMM with zero inflation, $\text{estimate}_{\text{stage}} = 0.063 \pm 0.154\text{SE}$, $p = 0.69$). Instead, factors predicting the number of birds seen in point-counts (Table 2 of Appendix 2.2) were the same than when only pre-playback counts were considered (Table 2).

Of 107 observations of groups or individual mynas, 56 responded to the sound of myna distress calls. Only the distance to the observer was shown to predict likelihood of mynas responding to the playback (Fig. 2, binomial GLMM, $\text{estimate}_{\text{distance-}} = -0.048 \pm 0.011\text{SE}$, $p < 0.01$, Table 4 of

Table 5 Minimum adequate model coefficients with log odds (*p* value of z-test) from Wald test indicating differences in probability. Because multiple comparison are taking place, the significance threshold was lowered to 0.005, significant factors are indicated in bold

Activity[a]	(Intercept)	Trapping pressure (low)	Region (Sydney)	Group size	Season (winter)
Walking	− 1.25 (0.002)	**− 1.32** (0.001)[b]	**1.53** (0.001)	− 0.02 (0.864)	**− 1.65** (< 0.001)
Calling	0.86 (< 0.001)	− 0.25 (0.225)	− 0.47 (0.018)	− 0.25 (0.010)	**− 0.58** (0.003)
Foraging	− 1.87 (< 0.001)	0.16 (0.624)	0.55 (0.076)	**0.20** (0.001)	− 0.63 (0.022)
Flying	0.15 (0.504)	− 0.21(0.298)	− 0.09 (0.663)	0.02 (0.729)	− 0.38 (0.047)

[a] Activity baseline category: standing still

[b] Sample interpretation of table: the log odds of mynas engaging in locomotion rather than standing still decreases by 1.32 under low trapping pressure compared to high trapping pressure. In other words, birds are less likely to be walking in low trapping areas than in high trapping areas

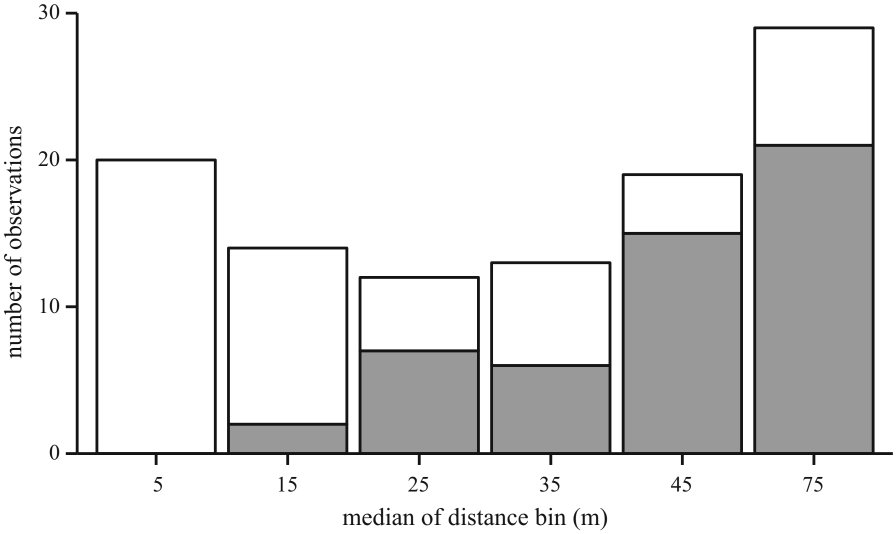

Fig. 2 Number of observations of groups of birds responding to playback (in white) or not responding to playback (in grey) as a function of the distance bin from the speaker at which birds were detected

Appendix 2.2). This suggests either that only birds closer to the stimulus responded to it, or that they were more likely to hear the stimulus.

Discussion

Common myna populations living under high and low risk of being trapped displayed differences in behaviour. Specifically, we found evidence that under high trapping pressure, mynas tended to form smaller groups, were more likely to stay close to refuges, and also tended to be less conspicuous. Interestingly the observed differences in behaviour were not a consequence of differences in myna abundance. On the other hand, trapping pressure failed to predict observed abundance.

We found no evidence that categorizing localities as high or low trapping pressure predicted the number of birds counted at a smaller spatial scale (i.e. 2 × 2 km SAs). Because we do not have data regarding abundance prior to capture efforts we cannot use this result to draw conclusions regarding effectiveness of trapping in reducing abundance. A recent study quantifying the impact of trapping pressure on myna population abundance in the Australian capital territory showed outcomes differed depending on the scale of analysis (Grarock et al. 2014). Variation in myna abundance calculated at a spatial scale approximately equal to that of locality used here was not predicted by variation in culling effort calculated at that scale. However, variation in myna abundance at finer spatial scales, approximately equal to that of SAs in the present study, was predicted by finer-scale variation in culling effort. Had data concerning abundance before control efforts been available to us, our results could have been taken to indicate that broad-scale trapping pressure does not predict fine-scale abundance. This would not be surprising as fine-scale movements within and between geographical units could easily influence local abundance. Overall, it seems more work to evaluate the effectiveness of trapping at different scales would be beneficial to common myna control.

The present analyses revealed that the number of common mynas seen was predicted by habitat, region and time of day. With regards to habitat, we found that mynas were more abundant in residential than highly urbanized habitats (e.g. high-density housing). This finding seems at odds with several other studies which have found that mynas are more abundant in more highly modified habitats including urban environments (White et al. 2005; Lowe et al. 2011; Sol et al. 2012). This discrepancy is likely attributable to the variety of methods used to categorize habitats across different studies. Here, habitat was defined at the scale of point-counts, however at the higher spatial scale of SAs, all our data can be considered to have been collected within residential suburban areas. In that light, our results indicate that within residential areas, mynas are more abundant in areas with intermediate levels of housing density and vegetation. This highlights the importance of spatial scale in categorizing habitats. A given location can be allocated to different habitat categories simply because parameters are calculated at different spatial scales (Marzluff et al. 2001).

Although group sizes observed in this study were small (1.86 individuals ± 1.66SE), they were similar to those found in the native range of common mynas (1.7 ± 0.1SE) (Burger and Gochfeld 1991). Notably, mynas tended to form larger groups more frequently in areas with low trapping pressure. At first, this finding seems at odds with the taxonomically widespread finding that group size increases under increasing predation risk (Caraco et al. 1980; Krause and Ruxton 2002), which is most often described in the context of actively hunting predators. Risks associated with traps, however, might be more akin to “sit-and-wait” predators that favor different anti-predator responses than those elicited by active predators (Preisser et al. 2007; Miller et al. 2014). Smaller groups, as observed in high-trapping environments, could reflect a strategy specific to traps. Indeed, within trapping communities, trapping is known to be most effective when caller birds are placed inside the trap to attract other birds. Therefore, a reduced tendency to aggregate might be advantageous because it reduces the tendency of individuals to approach trapped conspecifics, which in turn reduces their exposure to trapping risk.

Under high trapping pressure, mynas tended to be seen more often close to shelter. In general, many species prefer feeding close to a refuge if given the choice, presumably to limit predation risk (Slotow and Coumi 2000; Caro 2005). This supports our prediction that mynas have the potential to perceive high trapping environments as presenting a higher risk and to become more risk-averse. This view is also supported by the present finding that mynas showed a higher tendency to walk under high trapping pressure. Although it is expected that animals confronted to passive capture methods should decrease locomotion such that encounter with capture equipment is less likely (Alós et al. 2012), in mynas, increased locomotion has been associated with dangerous situations (Griffin and Boyce 2009). Overall, our findings are consistent with the possibility that high trapping areas are perceived by mynas as risky environments.

Behavioural differences associated with trapping pressure found here could potentially lead to further differences, in particular in terms of detectability. For example, the tendency to remain close to refuges under high trapping pressure means that these birds were closer to visual obstacles and hence could be harder to see for human observers. A similar phenomenon is apparent in game hunting, where more risk-averse pheasants tend to be less likely to be flushed from cover and hence seen and shot by hunters (Madden and Whiteside 2014). Additionally, smaller groups, as they appeared in high trapping localities, could be harder to detect for observers. Overall, this suggests there is scope for behaviour to affect detection of birds in high trapping areas.

In an effort to quantify potential differences in detectability across high and low trapping localities, we calculated an index based on the prediction that transect surveys would inflate abundance estimates compared to point-count surveys, particularly when mynas were conspicuous and at low density. While no effect of rarity was found, birds under high trapping pressure tended to have smaller inflation indexes than those under low trapping pressure. This finding is in line with an increase in crypticity in response to high trapping pressure such as that suggested by King (2010). It is also consistent with detectability changes found in other species. Lionfish populations that undergo control by spear-fishing shift their behaviour and activity patterns: they spend more time deeper in the reef, less time active during the day, and show high levels of concealment and avoidance of humans (Côté et al. 2014). These changes are likely to make the species more difficult to find and hence have the potential to hinder further control efforts (Côté et al. 2014). The trend towards less conspicuous birds in areas with high control pressure in common mynas is the first evidence that a similar phenomenon could be taking place in a bird species.

The fact that detectability of a bird species can be impacted by control pressure has important consequences for the way in which the success of these management programs is assessed. In North America, many migratory shorebird species have been declining since the 1980's, while raptors on the other hand have been on the rise. There is evidence that increased predation risk from raptors has caused shorebirds to alter their behaviour and spend less time at each stopover. Because abundance estimates are dependent on the duration of stay at each site, some authors argue that the perceived decline in shorebird populations does not reflect a true population decline but instead is due to changes in behaviour (Ydenberg et al. 2004; Ydenberg and Prins 2012). Similarly, a decrease in detectability in response to trapping would be of paramount importance in the context of pest bird control. Abundance estimates are often the only tool used to measure effectiveness of management (Wittenberg and Cock 2001). This suggests that, where changes in conspicuousness occur, there is scope for measured effectiveness of control to be overstated if specific survey methods that account for these types of effects are not implemented.

That trapping-induced reductions in detectability have scope to affect evaluations of myna management effectiveness is substantiated by the fact that control programs can lead to reductions in numbers that go well beyond the number of birds caught. Grarock et al. (2014) compared the number of mynas trapped by a community group in Canberra to density estimates before and after captures. The study showed that removal of 10–15 birds per km^2 could be associated with decreases of birds observed ranging from 20 to 50 birds per km^2. Although trapping-induced emigration and unreported catches might also contribute to the observed discrepancy, we suggest that changes in conspicuousness are also likely to play a role.

This study showed the first evidence of behavioural and detectability differences in common myna populations undergoing different trapping pressures. Such differences could originate from human-induced evolution, where some heritable behaviours may reduce likelihood of an individual being captured and may hence be selected for under high trapping pressure (Uusi-Heikkilä et al. 2008; Allendorf and Hard 2009; Ciuti et al. 2012). Under this scenario, behavioural changes would be necessarily adaptive, that is, reduce individual trapability. On the other hand behavioural differences could arise via experience-dependent cognitive processes, such as individual or social learning about dangerous stimuli (Griffin 2004; Brown and Chivers 2005), or plastic risk-dependent neophobia (Brown et al. 2013). In the case of common mynas, experience-dependent factors are particularly likely given a large body of existing research on this species' learning abilities (Griffin 2008; Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). Under this scenario, shifts in behaviour that ensue from learning or plasticity may or may not reduce individual trapability. Future work is needed to investigate adaptive function and proximate mechanism of the compensatory responses to trapping identified here.

Despite their far-reaching ramifications, behavioural shifts in response to control practices are still mostly overlooked. Yet, not only can behavioural changes alter management effectiveness directly, they may also modify the ecological impact of the invasive species. For instance, by making mynas emigrate towards novel habitats that may contain more native species. Such effects have been documented in lionfish, where changes in temporal and spatial activity patterns not only make them less susceptible to spear-fishing, but may also lead to increased interactions with other prey species that were not at risk of predation by lionfish previously (Côté et al. 2014). It is hence paramount that these behavioural changes are considered when management decisions are made.

Acknowledgements We would like to thank all local government areas and volunteer groups who took time to answer our questionnaires and share their data, in particular the Canberra Indian Myna Action Group (CIMAG). We would also like to thank Nils Hedouin for his assistance with the fieldwork.

Funding This work was financially supported by a grant from the Australian Pest Animal Research Program (APARP) and by a scholarship from the Wyong Shire Council and the University of Newcastle.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Data accessibility Data available on www.figshare.com.

References

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken

Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc Natl Acad Sci USA 106:9987–9994

Alós J, Palmer M, Arlinghaus R (2012) consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. PLoS ONE 7:1–9

Alós J, Palmer M, Trías P, Díaz-Gil C, Arlinghaus R (2014) Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. Can J Fish Aquat Sci 72:217–225

Arlinghaus R, Alós J, Klefoth T, Laskowski K, Monk CT, Nakayama S, Schröder A et al (2016) Consumptive tourism causes timidity, rather than boldness, syndromes: a response to Geffroy et al. Trends Ecol Evol 31:92–94

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bibby C, Jones M, Marsden S (1998) Expedition field techniques: bird surveys. Royal Geographical Society, London

Brown GE, Chivers DP (2005) Learning as an adaptative response to predation. In: Barbosa P, Castellanos I (eds) Ecology of predator–prey interactions. Oxford University Press, Oxford, pp 34–54

Brown GE, Ferrari MC, Elvidge CK, Ramnarine I, Chivers DP (2013) Phenotypically plastic neophobia: a response to variable predation risk. Proc R Soc Lond B Biol Sci 280:1–8

Burger J, Gochfeld M (1991) Human distance and birds: tolerance and response distances of resident and migrant species in India. Environ Conserv 18:158–165

Caraco T, Martindale S, Pulliam HR (1980) Avian flocking in the presence of a predator. Nature 285:400–401

Caro TM (2005) Antipredator defenses in birds and mammals. University of Chicago Press, London

Carthey AJR, Blumstein DT (2018) Predicting predator recognition in a changing world. Trends Ecol Evol 33:106–115

Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS (2012) Human selection of elk behavioural traits in a landscape of fear. Proc R Soc Lond B Biol Sci 279:4407–4416

Coltman DW, O'Donoghue P, Jorgenson JT, Hogg JT, Strobeck C, Festa-Bianchet M (2003) Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658

Conover MR (1994) Stimuli eliciting distress calls in adult passerines and response of predators and birds to their broadcast. Behaviour 131:19–37

Côté IM, Darling ES, Malpica-Cruz L, Smith NS, Green SJ, Curtis-Quick J, Layman C (2014) What doesn't kill you makes you wary? Effect of repeated culling on the behaviour of an invasive predator. PLoS ONE 9:e94248

Feare C, Craig A (1999) Common myna, *Acridotheres tristis*. In: Feare C, Craig A (eds) Starlings and mynas. Princeton University Press, Princeton, pp 157–160

Fenberg PB, Roy K (2008) Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Mol Ecol 17:209–220

Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim Methods Softw 27:233–249

Grarock K, Tidemann CR, Wood JT, Lindenmayer DB (2012) Is it benign or is it a Pariah? Empirical evidence for the impact of the common myna (*Acridotheres tristis*) on Australian birds. PLoS ONE 7:e40622

Grarock K, Tidemann CR, Wood JT, Lindenmayer DB (2014) Understanding basic species population dynamics for effective control: a case study on community-led culling of the common myna (*Acridotheres tristis*). Biol Invasions 16:1427–1440

Griffin AS (2004) Social learning about predators: a review and prospectus. Learn Behav 32:131–140

Griffin AS (2008) Social learning in Indian mynahs, *Acridotheres tristis*: the role of distress calls. Anim Behav 75:79–89

Griffin AS (2009) Temporal limitations on social learning of novel predators by Indian mynahs, *Acridotheres tristis*. Ethology 115:287–295

Griffin AS, Boyce HM (2009) Indian mynahs, *Acridotheres tristis*, learn about dangerous places by observing the fate of others. Anim Behav 78:79–84

Griffin AS, Haythorpe K (2011) Learning from watching alarmed demonstrators: does the cause of alarm matter? Anim Behav 81:1163–1169

Griffin AS, Blumstein DT, Evans CS (2000) Training captive-bred or translocated animals to avoid predators. Conserv Biol 14:1317–1326

Griffin AS, Evans CS, Blumstein DT (2001) Learning specificity in acquired predator recognition. Anim Behav 62:577–589

Griffin AS, Boyce HM, MacFarlane GR (2010) Social learning about places: observers may need to detect both social alarm and its cause in order to learn. Anim Behav 79:459–465

King DH (2010) The effect of trapping pressure on trap avoidance and the role of foraging strategies in anti-predator behaviour of common mynas (*Sturnus tristis*). Canberra Bird Notes 35:85–108

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford

Kuparinen A, Merilä J (2007) Detecting and managing fisheries-induced evolution. Trends Ecol Evol 22:652–659

Le Saout S, Padié S, Chamaillé-Jammes S, Chollet S, Côté S, Morellet N, Pattison J, Harris E, Martin J-L (2014) Short-term effects of hunting on naïve black-tailed deer (*Odocoileus hemionus sitkensis*): behavioural response and consequences on vegetation growth. Can J Zool 92:915–925

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lowe S, Browne M, Boudjelas M, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. Auckland, Invasive Species Specialist Group (SSC/IUCN), p 12

Lowe K, Taylor C, Major R (2011) Do common mynas significantly compete with native birds in urban environments? J Ornithol 152:909–921

Madden JR, Whiteside MA (2014) Selection on behavioural traits during 'unselective' harvesting means that shy pheasants better survive a hunting season. Anim Behav 87:129–135

Marzluff JM, Bowman R, Donnelly R (2001) A historical perspective on urban bird research: trends, terms, and approaches. In: Marzluff J, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Springer, New York, pp 1–17

Miller JRB, Ament JM, Schmitz OJ (2014) Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. J Anim Ecol 83:214–222

Ordiz A, Støen O-G, Sæbø S, Kindberg J, Delibes M, Swenson JE (2012) Do bears know they are being hunted? Biol Conserv 152:21–28

Peacock DS, van Rensburg BJ, Robertson MP (2007) The distribution and spread of the invasive alien common myna, *Acridotheres tristis* L. (Aves: Sturnidae), in southern Africa. S Afr J Sci 103:465–473

Pell AS, Tidemann CR (1997) The impact of two exotic hollow-nesting birds on two native parrots in savannah and woodland in eastern Australia. Biol Conserv 79:145–153

Pigeon G, Festa-Bianchet M, Coltman DW, Pelletier F (2016) Intense selective hunting leads to artificial evolution in horn size. Evol Appl 9:521–530

Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. Ecology 88:2744–2751

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Slotow R, Coumi N (2000) Vigilance in Bronze Mannikin Groups: the contributions of predation risk and intra-group competition. Behaviour 137:565–578

Sol D, Bartomeus I, Griffin A (2012) The paradox of invasion in birds: competitive superiority or ecological opportunism? Oecologia 169:553–564

Sullivan AP, Bird DW, Perry GH (2017) Human behaviour as a long-term ecological driver of non-human evolution. Nat Ecol Evol 1:0065

Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R (2008) A behavioral perspective on fishing-induced evolution. Trends Ecol Evol 23:419–421

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, New York

White JG, Antos MJ, Fitzsimons JA, Palmer GC (2005) Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. Landsc Urban Plan 71:123–135

Wittenberg R, Cock MJ (2001) Invasive alien species: a toolkit of best prevention and management practices. CABI, Wallingford

Ydenberg R, Prins H (2012) Foraging. In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world. Oxford University Press, Oxford

Ydenberg RC, Butler RW, Lank DB, Smith BD, Ireland J (2004) Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. Proc R Soc Lond B Biol Sci 271:1263–1269

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Zero-truncated and zero-inflated models for count data. In: Mixed effects models and extensions in ecology with R. Springer, Berlin, pp 261–293