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Demography, traits and vulnerability to urbanization: can we make generalizations?

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Summary

1. Human-induced land cover change threatens species diversity and ecosystem services. The rapid pace of current change makes predicting species' declines imperative, but leaves little time for thorough study of all species. One solution is to make generalizations about species' vulnerability to urbanization based on traits common among studied species in decline.

2. To date, most generalizations about traits associated with species' declines in response to urbanization are based on presence or abundance, or detailed studies of a few species. If these generalizations broadly reflect responses to urbanization, they should hold across the mechanisms driving patterns of abundance, such as survival or reproduction.

3. Across 68 bird species in the north-eastern USA, we investigated how food preference, nest location, habitat preference, migration distance, number of broods, clutch size, body mass and an interaction between urbanization and these traits affected survival and reproduction.

4. Mass was the strongest predictor of survival, followed by number of broods, migration distance and nest location. Nest location was the strongest predictor of reproduction, followed by migration distance. No interaction between urbanization and species' traits affected survival; however, differences in response to urbanization among species with different food preferences, migration distances, masses, nest locations and number of broods were important in predicting reproduction.

5. *Synthesis and applications*. We found that some traits influenced demographic rates even though they were not associated with urbanization; identifying differences in species' baseline demographic rates, irrespective of urbanization, is needed to guide management objectives. Reproduction, but not survival, was influenced by urbanization, suggesting that management in our region of study should target increasing suitable nest sites and reducing nest predation. Determining traits associated with demographic rates and urbanization across broad geographic extents can provide new insights for species' management and help guide conservation initiatives.

Key-words: birds, conservation, demography, environmental filtering, human disturbance, life-history, reproduction, survival, traits, urbanization

Introduction

There is little argument that human alteration of landscapes negatively impacts species and drives local extinctions. Losses of biodiversity and ecosystem services marked by biotic homogenization have been extensively studied over the past decade, showing clear patterns across multiple taxa (Lockwood & McKinney 2001; McKinney 2006). At the same time, a few species successfully exploit and thrive in areas of urbanization (Marzluff 2001; Devictor *et al.* 2008; McKinney 2008). Minimizing negative effects of habitat fragmentation and urbanization requires knowing which species are affected, and creating policies that will protect or create habitat suitable for more vulnerable species. Studying every species' response to urbanization is clearly not possible. As an alternative to studying all species, life-history traits shared among species with known negative responses can be used to make inferences about the types of species that will be negatively affected by urbanization. These inferences, however, are

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often based on compiling results of single-species or few-species studies, or studies limited in geographic scope or levels of urbanization, such that broad generalizations are difficult to make (Blumstein *et al.* 2005; Pautasso *et al.* 2011).

The concept of *environmental filtering* (Keddy 1992; Mayfield, Boni & Ackerly 2009), whereby human-disturbed areas can be thought of as filters that allow only species with certain characteristics to persist (Lizee *et al.* 2011), has recently been used to evaluate which species will persist in disturbed landscapes. Environmental filtering can aid in determining if abundance or richness of species found in urban to rural environments is driven by a shared set of life-history traits (e.g. Clergeau *et al.* 2006; Kark *et al.* 2007; Croci, Butet & Clergeau 2008; Evans *et al.* 2011; Lizee *et al.* 2011; Hanspach *et al.* 2012). While this approach can be useful for predicting which species may be affected by human-induced land-use changes (Hanspach *et al.* 2012), it does not get at the underlying mechanisms driving patterns of presence and abundance. If traits associated with species' presence or abundance in urbanizing landscapes represent truly generalizable patterns, we expect these same relationships to exist between demographic parameters and traits, because species' presence and abundance are driven by survival and site fidelity (collectively, apparent survival), reproduction and their combined effect on species' persistence (Saracco, Desante & Kaschube 2008).

We used mark–recapture data from Monitoring Avian Productivity and Survivorship (MAPS) data (Desante *et al.* 1995) to test whether generalizations reported in the literature about traits influencing species' responses to urbanization also predict differences in survival and reproduction across sites of varying levels of urbanization. Demographic data can be difficult and time-consuming to obtain, making our study novel in having ample data to investigate the relationship between traits and demographic parameters across a geographic region spanning rural to urban landscapes. The numerous studies of avian responses to human-disturbed landscapes and fragmentation make birds a model taxon on which to test generalizations about the relationship between life-history traits and demography. We define *trait* broadly as ecological or life-history characteristics that differ among species and may contribute to variation in response to urbanization. The traits that we predicted would influence apparent survival and reproduction were nest location, food preference, habitat preference, migration distance, number of possible brood attempts, clutch size and body mass.

We summarize our predictions about how survival or reproduction may be affected by urbanization across groups of species in Table 1. First, we expected ground-nesting species to be negatively affected by urbanization and to have lower demographic rates than cavity or tree-nesting species (e.g. Gilbert 1989; Jokimäki & Huhta 2000; Evans *et al.* 2011), due to increases in cats and avian predators with urbanization (Lepczyk, Mertig & Liu 2004b; van Heezik *et al.* 2010; Balogh, Ryder & Marra 2011; Stracey 2011). We expected cavity-nesting species, on the other hand, might benefit from urbanization, especially secondary nesters which may utilize urban nest boxes (Lepczyk, Mertig & Liu 2004a; LeClerc *et al.* 2005). Secondly, we expected insectivores to be negatively affected by urbanization because both specialized species and diversity and abundance of invertebrate prey tend to decrease with urbanization (Paul & Meyer 2001; Devictor *et al.* 2007; Devictor, Julliard & Jiguet 2008; McKinney 2008; Evans *et al.* 2011). We expected omnivores to have higher apparent survival and reproduction with urbanization because these species are more prevalent in urban areas (Chace & Walsh 2006; Kark *et al.* 2007) and may benefit from human subsidies (e.g. birdfeeders). Thirdly, we expected forest species to have lower survival than edge species because forest species decline with urban-associated fragmentation, and edge species generally thrive (Chace & Walsh 2006). Fourthly, we expected resident species to have higher survival and reproduction than short- or long-distance migrants because they can respond to local scale environmental variables, exploit resources and establish territories before migrants arrive (Both *et al.* 2010). Urban food subsidies may also increase survival for residents during harsh winters and improve breeding success in the following season (Robb *et al.* 2008). Fifth, we expected species with larger clutches or more than one brood per season to have higher reproductive success in urban areas than those with smaller clutches or only a single brood per season (Reale & Blair 2005). Finally, we expected apparent survival in larger-bodied species to be lower than in smaller-bodied species due to the negative association between body size and human presence (Blumstein *et al.* 2005; Blumstein 2006; Vargas *et al.* 2012). We expected that some characteristics such as nest location, number of broods and clutch size might have a greater effect on reproduction than on survival, but could indirectly influence apparent survival because site fidelity is influenced by reproductive success (Haas 1998). We evaluated our predictions in 68 bird species in the north-eastern USA to determine whether the patterns found in studies of abundance and richness are confirmed in this analysis of demographic measures.

Materials and methods

BIRD-RINGING (BANDING) DATA AND SITES

We obtained MAPS bird-ringing data from the Institute for Bird Populations (Desante *et al.* 1995). The data we used were collected across 98 sites in the north-eastern USA (Maine, Vermont, New Hampshire, Massachusetts, Connecticut, New York, Pennsylvania, New Jersey, Delaware, Rhode Island) for 4–19 years spanning 1989–2007. These sites cover 20 hectare or larger, typically wooded or semi-wooded areas, in which mist-nets are placed and birds are ringed (banded) according to a standard-effort

Table 1. Expected and observed effects of housing density (HD) on survival (*s*) and maternity (*m*, our metric for reproduction) across traits, and expected and observed direction of relationship among traits. Observed relationships reflect trends from visualization of full models only

Group	Trait	Expected effect of HD	Observed effect of HD	Expected relationship	Observed relationship(s)
Nest location	Cavity (C)	+	None found	G < S or C	G > S (*s*) S < C or G (*m*)
	Shrub/tree (S)	NA	− (*m*)		
	Ground (G)	−	None found		
Food preference	Omnivores (O)	+	+ (*m*)	O > I	I > O
	Insects/other (V)	NA	None found		
	Insectivores (I)	−	− (*m*)		
Habitat preference	Forest (F)	−	None found	F < E	None found
	Edge (E)	+	None found		
Migration distance	Resident (R)	+	− (*m*)	R > SD or LD	LD > SD (*s*) R > SD or LD (*m*)
	Short-distance (SD)	NA	None found		
	Long-distance (LD)	NA	None found		
Number of broods	>1 brood	+	None found	More than one brood > single brood	More than one brood < single brood (*s*)
	Single brood	−	− (*m*)		
Clutch size	Small clutch	+	None found	Smaller clutches > larger clutches	None found
	Large clutch	−	None found		
Mass	Small (10–20 g)	+	− (*m*)	Smaller mass < larger mass	Smaller mass < larger mass (*s*); Larger mass < smaller mass (*m*)
	Large (40–100 g)	−	+ (*m*)		

protocol (Desante *et al.* 1995, 2012). We verified the recorded latitude and longitude for each site based on the overall vegetation structure recorded by site operators, and site names compared with similarly named landmarks (e.g. parks) using Google Earth, *Version 5.2* (build date September 1, 2010). We adjusted coordinates of twelve of the 98 sites, all by less than 1 km, based on personal visits, or to place sites within boundaries of the closest area with vegetation consistent with that recorded by site operators (e.g. deciduous forest as opposed to water or city streets). We created a 1-km buffer around each site to account for GPS imprecision and to encompass variation in human-developed land cover surrounding sites. We combined sites located less than 1-km apart in which buffers overlapped by more than 10%. Fifteen of 98 total bird-ringing sites were combined, 12 into pairs and three into one group.

URBANIZATION DATA

We used USA housing density data for the year 2000 from the SILVIS laboratory of the University of Wisconsin (http://silvis.forest.wisc.edu/) as our metric of urbanization. The spatial resolution of these data ranges from 1·80 to 3·93 km^2 (Hammer *et al.* 2004). The 1-km buffer encompassing a single MAPS site may include more than one partial block group, the unit within which housing density is estimated from census data. Therefore, we calculated a weighted average of housing density based on the proportion of each site's buffer that fell within each partial block group. We assumed a high correlation between housing density and human population (Lepczyk *et al.* 2008), so did not use population data as an additional predictor variable.

PARAMETER ESTIMATES

We estimated apparent survival of adult (after-hatch-year) birds using the Cormack–Jolly–Seber (CJS) model in Program MARK (White & Burnham 1999). Prior to estimating survival, we deleted dead and injured individuals from the capture history data because these individuals were not likely to be recaptured at later time periods. We did not include data from sites that did not have at least one recapture record during years of operation.

We estimated survival for each species at each site it was present as a single constant estimate per site, or varying by age (hatch-year survival differs from after-hatch-year survival) and/or time since marking (allowing the first capture event to differ from subsequent events to account for transient individuals; Pradel *et al.* 1997). We allowed recapture to vary by site, age and/or time, or to be a constant, single value (expected for a sampling-wide constant-effort protocol). We used adult (after-hatch-year) survival estimates for each species at each site from the CJS model with the lowest Akaike Information Criterion (AIC). We did not perform goodness-of-fit tests because our data contained missing years, and there is currently no robust way to estimate overdispersion for incomplete data (e.g. following Danner *et al.* 2013).

For each species at each site for which survival was estimated, we used maternity as our metric for reproduction. We calculated maternity as:

$$\frac{f_1 + f_2 + f_3 + \ldots f_n}{N_1 + N_2 + N_3 + \ldots N_n} \qquad \text{eqn 1}$$

where f is the number of juveniles captured in years 1 to n, and N is the number of adults captured in years 1 to n. Maternity values are weighted averages (maternity, f/N, weighted by sample size, N, for each year) to account for variation in effort across time steps, such that estimates of maternity from years with small N contribute less to time-averaged estimates (H. R. Akçakaya, *pers. comm*). The 68 species for which both survival and maternity were estimated here fall within 12 families across 85 sites ($N = 820$ data points, where each datum represents a single species at a single site).

SPECIES CHARACTERISTICS

We obtained life-history information for all species from the Birds of North America (BNA) online data base (Poole 2005) and Valiela & Martinetto (2007). We grouped species by nest location (cavity, shrub/tree or ground/near ground), food preference [omnivore, insectivore, or insects and either fruits or seeds (hereafter insects/other)], habitat preference during the breeding season (forest or edge), number of broods (1 or >1), migration distance (resident, short distance, long distance), mean clutch size (rounded to the nearest 0·5) and mean body mass (Table S1, Supporting information). We obtained mean body mass for breeding populations within our study region from the BNA and the CRC Handbook of Avian Masses (Dunning 2007). Mass is averaged across males and females, as this was the only value available for some species.

PHYLOGENETIC DATA

We obtained published phylogenies of our 68 focal species from Zink & Johnson (1984), Johnson, Zink & Marten (1988), Benz, Robbins & Peterson (2006), Jønsson & Fjeldså (2006), Treplin *et al.* (2008), Tello *et al.* (2009), Lovette *et al.* (2010) and Powell *et al.* (2014). We combined these phylogenies to build a phylogenetic tree using Mesquite, version 3.01 (Maddison & Maddison 2014; Fig. S1). We specified ultrametric branch lengths, which assume equal time along branch lengths to a common ancestor (e.g. following Lee *et al.* 2008).

STATISTICAL ANALYSES

We evaluated the direct relationship between life-history traits and demographic rates by testing for an effect of nest location, food preference, habitat preference, migration distance, number of broods, clutch size or mass on each of survival and reproduction. We determined if there was a relationship between these traits and urbanization by testing for interactions between traits and housing density on each of survival and reproduction; including the interaction term also tests for a direct effect of housing density on survival and reproduction. We used mixed-effects models in the R (R Core Team 2014) package 'lme4' (Bates *et al.* 2014) and ran a full model and all model subsets containing each predictor and its interaction with housing density using the dredge function in the R package 'MuMIn' (Bartón 2014). We summarized the results of all models within ΔAIC<4 (i.e. the top models) from the dredge procedure using Wald chi-square tests ('ANOVA' function in the R package 'car'; Fox & Weisberg 2011). We evaluated predictor importance based on the proportion of top models in which an effect was significant in Wald tests. We visualized the relationship between levels within individual predictors that were significant in top models by plotting their effect in the full model using the R package 'effects' (Fox 2003). In all models, housing density, mass and clutch size were log-transformed, survival was logit-transformed, and species and site were random effects. Survival was weighted by 1/standard error to account for unequal variances among estimates from Program MARK. Maternity, our metric for reproduction, simplifies to the number of hatch-year birds (nHY) divided by number of after-hatch-year birds (nAHY) for each site. Thus, to evaluate reproduction, we regressed nHY on predictor variables using a Poisson generalized linear mixed-effects model (GLMM) with a log link, and an offset of log (nAHY). This more accurately reflects the data because a maternity value of 0·5 for a site with 10 : 20 nHY : nAHY birds of a particular species is not treated the same as a value at a site where this ratio is 100 : 200. There was little difference in survival or reproduction between primary and secondary cavity nesters, hence, cavity nesters were combined in our analyses. We found no evidence of spatial autocorrelation in response variables based on Moran's *I*.

We tested for phylogenetic signal, estimated as $\frac{\mathrm{var(phylo)}}{\mathrm{var(phylo)+var(residual)+var(randomefects)}}$ (following Hadfield & Nakagawa 2010), by running models with all predictors in the 'MCMCglmm' package (Hadfield 2010). Phylogenetic signal was low (0·003 and 0·009 in models predicting survival and reproduction, respectively; one indicates phylogenetic signal, and zero indicates no signal), and coefficients were similar from models run in 'MCMCglmm' vs. the 'lme4' package, indicating that accounting for phylogeny was not necessary (Table S2). Given negligible phylogenetic signal, we ran all models using the R package 'lme4' because it enables inclusion of weights and offsets, not available in the 'MCMCglmm' package.

Results

Mass predicted survival in all 14 top models ($P \leq 0{\cdot}0001$ in 12 of 14 models, $P \leq 0{\cdot}001$ in 1 of 14 models, $P \leq 0{\cdot}01$ in 1 of 14 models), followed by number of broods in 6 of 14 models ($P \leq 0{\cdot}01$ in 5 of 14 models, $P \leq 0{\cdot}05$ in 1 of 14 models), migration distance in 4 of 14 models ($P \leq 0{\cdot}01$ in 2 of 14 models, $P \leq 0{\cdot}05$ in 2 of 14 models) and nest location in 1 of 14 models ($P \leq 0{\cdot}05$ in 1 of 14 models; Table 2). Clutch size and habitat preference were also included in top models, but were not significant predictors, and there were no effects of housing density on survival.

Our metric for reproduction (maternity) was predicted in all 34 of the top models by nest location ($P \leq 0{\cdot}0001$ in 34 of 34 models), an interaction between housing density and food preference ($P \leq 0{\cdot}0001$ in 34 of 34 models) and an interaction between housing density and migration distance ($P \leq 0{\cdot}0001$ in 27 of 34 models, $P \leq 0{\cdot}001$ in 7 of 34 models; Table 3). An interaction between housing density and mass predicted maternity in 26 of 34 models ($P \leq 0{\cdot}0001$ in 4 of 34 models, $P \leq 0{\cdot}001$ in 6 of 34 models, $P \leq 0{\cdot}01$ in 15 of 34 models, $P \leq 0{\cdot}05$ in 1 of 34 models), followed by migration distance alone in 24 of 34 models ($P \leq 0{\cdot}05$), an interaction between housing density and nest location in 10 of 34 models ($P \leq 0{\cdot}05$) and an interaction between housing density and number of broods in 4 of 34 models ($P \leq 0{\cdot}05$; Table 3). All other predictors were present in some combination of the models, but were not significant predictors in the model summary.

In the full model predicting survival, there was a positive effect of mass, having only one brood, and being a long-distance migrant or ground-nester relative to being a short-distance migrant or shrub/tree nester, respectively (Figure 1). In the full model predicting maternity, there was a negative effect of being a shrub/tree nester and a

Table 2. Variables present in top models predicting survival; M, mass; Br, number of broods; Mig, migration distance; N, nest location; Cl, clutch size; Hab, preferred habitat

					Significance level of predictors (ns = non-significant)				
	d.f.	AICc	ΔAICc	Weight	M	Br	Mig	N	Other ns predictors
1	6	2015·84	0	0·23	≤0·0001	≤0·01			
2	7	2016·76	0·91	0·15	≤0·0001	≤0·01			Cl
3	8	2018·03	2·19	0·08	≤0·0001	≤0·05	*ns*		
4	9	2018·48	2·64	0·06	≤0·0001		≤0·01	≤0·05	
5	7	2018·65	2·81	0·06	≤0·0001		≤0·05		
6	10	2018·73	2·89	0·06	≤0·0001	≤0·10	*ns*	*ns*	
7	8	2018·79	2·95	0·05	≤0·0001	≤0·01		*ns*	
8	5	2018·92	3·08	0·05	≤0·001				
9	8	2018·99	3·14	0·05	≤0·0001		≤0·05		Cl
10	9	2018·99	3·14	0·05	≤0·0001	≤0·01		*ns*	Cl
11	9	2019·17	3·33	0·04	≤0·0001	≤0·10	*ns*		Cl
12	7	2019·18	3·33	0·04	≤0·01	≤0·01			Hab
13	10	2019·37	3·53	0·04	≤0·0001		≤0·01	*ns*	Cl
14	11	2019·46	3·61	0·04	≤0·0001	≤0·10	*ns*	*ns*	Cl

positive effect of being a resident species, insectivore, or having a smaller mass on maternity (Figure 2). The direction of the effect of housing density on maternity was positive in omnivores and birds with larger masses, and negative in shrub/tree nesters, insectivores, resident species, species with a single brood relative to those with more than one brood and birds with smaller masses (Figure 2).

Discussion

Predicting how species respond to anthropogenic disturbances is essential for ensuring their conservation and maintaining ecosystem services. Across a broad geographic region with varying levels of urbanization (Radeloff *et al.* 2005), we found differences in demographic rates among traits, but not always in response to urbanization. This result emphasizes the importance of distinguishing pre-existing differences among traits from those in response to urbanization (Evans *et al.* 2011). Management initiatives should target species with traits that appear to be negatively influenced by urbanization, but should also closely monitor species with traits that more generally appear to confer lower rates of survival or reproduction. In addition, we found that urbanization affected reproduction more than survival, consistent with previously reported effects of urbanization on reproductive success (e.g. Chace & Walsh 2006; Chamberlain *et al.* 2009). Given this result, identifying and mitigating factors negatively influencing reproductive success in urban environments, for instance by providing nest sites or reducing nest predation, may be a useful management approach (Kight & Swaddle 2007; Balogh, Ryder & Marra 2011). While we find clear patterns for north-eastern North American birds, we caution against generalizing this result to all regions and taxa. For instance, lower nest predation in Europe than North America (Martin & Clobert 1996) may differentially impact the relationship between traits and reproduction in urban areas. In addition, abundance may be sufficient for evaluating responses to urbanization in highly productive taxa such as insects (Williams *et al.* 2010), while demographic measures may be more useful for longer-lived taxa. Ideally, our approach can be used as a guide to study other regions and taxa in the hope that broad generalizations emerge that will be useful to management.

Food preference, mass, migration distance and nest location were particularly important in predicting species' responses to urbanization. Our analyses appear to confirm our expectation that strict insectivores are likely negatively affected by urbanization, though this result conflicts with one of a few previous large-scale evaluations of how traits affect responses to urbanization, which found that densities of ground-nesters, but not insectivores, declined with urbanization in Great Britain (Evans *et al.* 2011). In contrast, we observed a negative effect of urbanization on shrub/tree nesters. Similarly, mass has been argued to be a proxy for species' responses to human disturbance (Blumstein *et al.* 2005; Blumstein 2006), but our findings were the opposite of what we expected. We expected that larger species might have lower demographic rates with urbanization because they are more wary of human presence (Blumstein 2006), so may invest less in reproduction in these areas. Conversely, smaller species with larger clutches and shorter life spans, for example 'fast-living' species, might be more resilient to human disturbance because they invest in reproduction at the cost of their own survival, and are less likely to flee disturbance at the expense of their offspring (Bisson *et al.* 2009). In contrast, we saw a negative trend in the effect of urbanization on reproduction in smaller-bodied species and a positive trend in the effect on larger-bodied species. The greater flight-initiation distance of larger birds (Blumstein 2006) could reflect greater vigilance, making them less likely to put their young in danger by nesting or foraging in the

Table 3. Variables present in top models predicting maternity, our metric for reproduction; N, nest location; Mig, migration distance; HD, housing density; Fd, food preference; M, mass; Br, number of broods; Cl, clutch size; Hab, preferred habitat

					Significance level of predictors (ns = non-significant)							
	d.f.	AICc	ΔAICc	Weight	N	Mig	HD × Fd	HD × Mig	HD × M	HD × N	HD × Br	Other ns predictors
1	20	9545·16	0	0·09	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·01	≤0·05	*ns*	Fd, M, Br, HD
2	18	9545·41	0·25	0·08	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·001	*ns*		Fd, M, HD
3	20	9545·83	0·67	0·07	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·0001	≤0·05		Fd, M, Hab, HD, HD × Hab
4	16	9546·1	0·94	0·06	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·01			Fd, M, HD
5	21	9546·51	1·35	0·05	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·01	≤0·05	*ns*	Fd, M, Br, Cl, HD
6	19	9546·64	1·48	0·04	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·001	*ns*		Fd, M, Br, HD
7	21	9546·86	1·7	0·04	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·01	≤0·05	*ns*	Fd, M, Br, Hab, HD
8	21	9546·94	1·78	0·04	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·0001	≤0·05		Fd, M, Br, Hab, HD × Hab
9	22	9547·2	2·03	0·03	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·01	≤0·05	ns	Fd, M, Br, Hab, HD × Hab
10	19	9547·25	2·09	0·03	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·001	*ns*		Fd, M, Hab, HD
11	16	9547·28	2·11	0·03	≤0·0001	≤0·05	≤0·0001	≤0·0001			≤0·05	Fd, Br, HD
12	17	9547·31	2·14	0·03	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·01			Fd, M, Br, HD
13	19	9547·42	2·25	0·03	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·001	*ns*		Fd, M, Cl, HD
14	18	9547·48	2·31	0·03	≤0·0001	≤0·05	≤0·0001	≤0·0001		*ns*	≤0·01	Fd, Br, HD
15	21	9547·85	2·69	0·02	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·0001	≤0·05		Fd, M, Hab, Cl, HD, HD × Hab
16	17	9547·91	2·74	0·02	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·01			Fd, M, Hab, HD
17	18	9547·93	2·77	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001	*ns*		ns	Fd, M, Br, HD
18	20	9548·04	2·88	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·001	*ns*		Fd, M, Br, Cl, HD
19	17	9548·08	2·91	0·02	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·01			Fd, M, Cl, HD
20	22	9548·13	2·97	0·02	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·01	≤0·05	*ns*	Fd, M, Br, Hab, Cl
21	17	9548·29	3·12	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001			≤0·05	Fd, Br, Cl, HD
22	22	9548·3	3·13	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·0001	≤0·05		Fd, M, Br, Hab, Cl, HD × Hab
23	20	9548·34	3·18	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·001	*ns*		Fd, M, Br, Hab, HD
24	23	9548·5	3·34	0·02	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·01	≤0·05	*ns*	Fd, M, Br, Hab, Cl, HD × Hab
25	18	9548·51	3·35	0·02	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·01			Fd, M, Hab, HD × Hab
26	19	9548·54	3·37	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001		*ns*	≤0·01	Fd, Br, Cl, HD
27	22	9548·62	3·46	0·02	≤0·0001	≤0·05	≤0·0001	≤0·001	≤0·05	*ns*	*ns*	Fd, M, Br, Cl, HD × Cl
28	18	9548·63	3·46	0·02	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·01			Fd, M, Br, Cl, HD
29	20	9548·67	3·5	0·02	≤0·0001	*ns*	≤0·0001	≤0·0001	≤0·01	*ns*		Fd, M, Cl, HD × Cl
30	17	9548·85	3·69	0·01	≤0·0001	≤0·05	≤0·0001	≤0·0001			≤0·05	Fd, M, Br, HD
31	17	9548·86	3·7	0·01	≤0·0001	≤0·05	≤0·0001	≤0·0001			≤0·05	Fd, M, Br, HD
32	18	9548·98	3·81	0·01	≤0·0001	≤0·05	≤0·0001	≤0·0001	≤0·01			Fd, M, Br, Hab, HD
33	19	9549·1	3·94	0·01	≤0·0001	≤0·05	≤0·0001	≤0·0001		*ns*	≤0·01	Fd, Br, Hab, HD
34	19	9549·12	3·96	0·01	≤0·0001	≤0·05	≤0·0001	≤0·0001		*ns*	≤0·01	Fd, M, Br, HD

presence of predators (Frid & Dill 2002). Larger birds may also be more aggressive towards nest predators (Larsen, Sordahl & Byrkjedal 1996), and greater cognitive abilities may make them more resilient to the presence of humans (Reif *et al.* 2011). Finally, our results suggest that residents are negatively affected by urbanization, in contrast to our expectation that they would be able to adapt to new conditions and respond positively because of food supplements, although omnivores did respond positively. These results imply that urban conservation initiatives should target smaller-bodied species, in particular those that are specialist species such as insectivores, and residents. Monitoring and future study of other specialist-feeding species, such as granivores, would be a valuable contribution.

We found some relationships between demographic rates and traits that were not in response to urbanization. For instance, mass, number of broods, migration distance and nest location were important in predicting survival, and nest location and migration distance in predicting reproductive success. Several of these findings are consistent with expectations based on life-history trade-offs (Stearns 1992). Mass was the strongest predictor of survival, with larger species having higher survival and lower reproduction, and smaller species having lower survival and higher reproduction. Similarly, species with more than one brood per season (i.e. more resources invested into reproduction) had lower survival than species with a single brood. Nest location was the strongest predictor of reproduction, possibly reflecting high rates of avian nest predation on species with more open, visible nests (Luginbuhl *et al.* 2001), though avian nest predation is a threat in urban areas as well (Jokimäki & Huhta 2000). Species with traits that confer lower rates of survival or reproduction should be monitored more closely in urbanizing areas, and additional research should focus on why these traits may increase risks of species' decline.

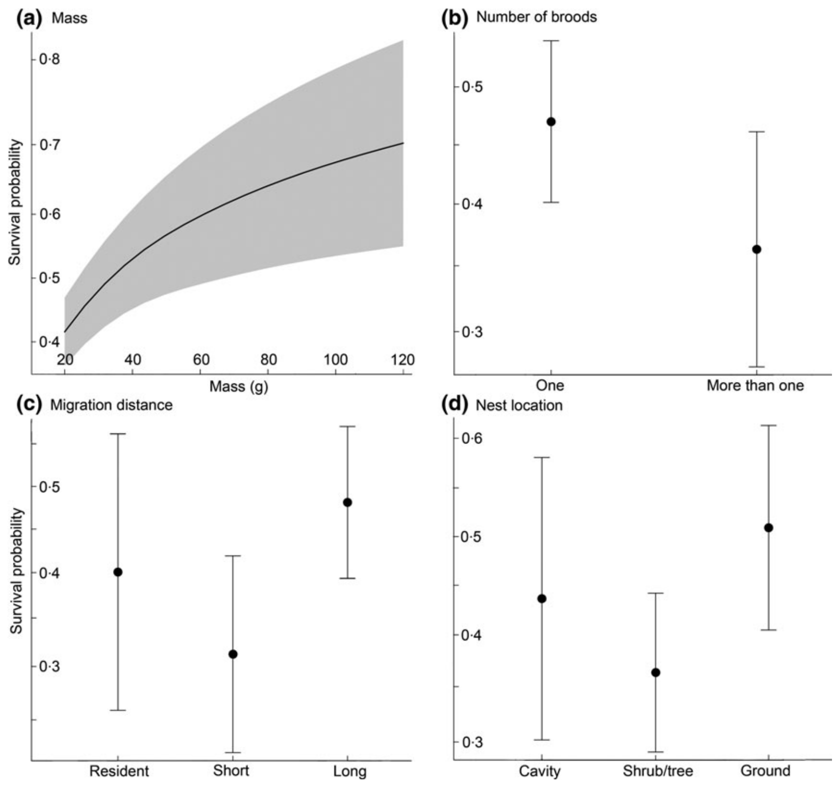

Fig. 1. Back-transformed means and 95% confidence intervals depicting the relationship between survival and (a) mass, (b) number of broods, (c) migration distance and (d) nest location.

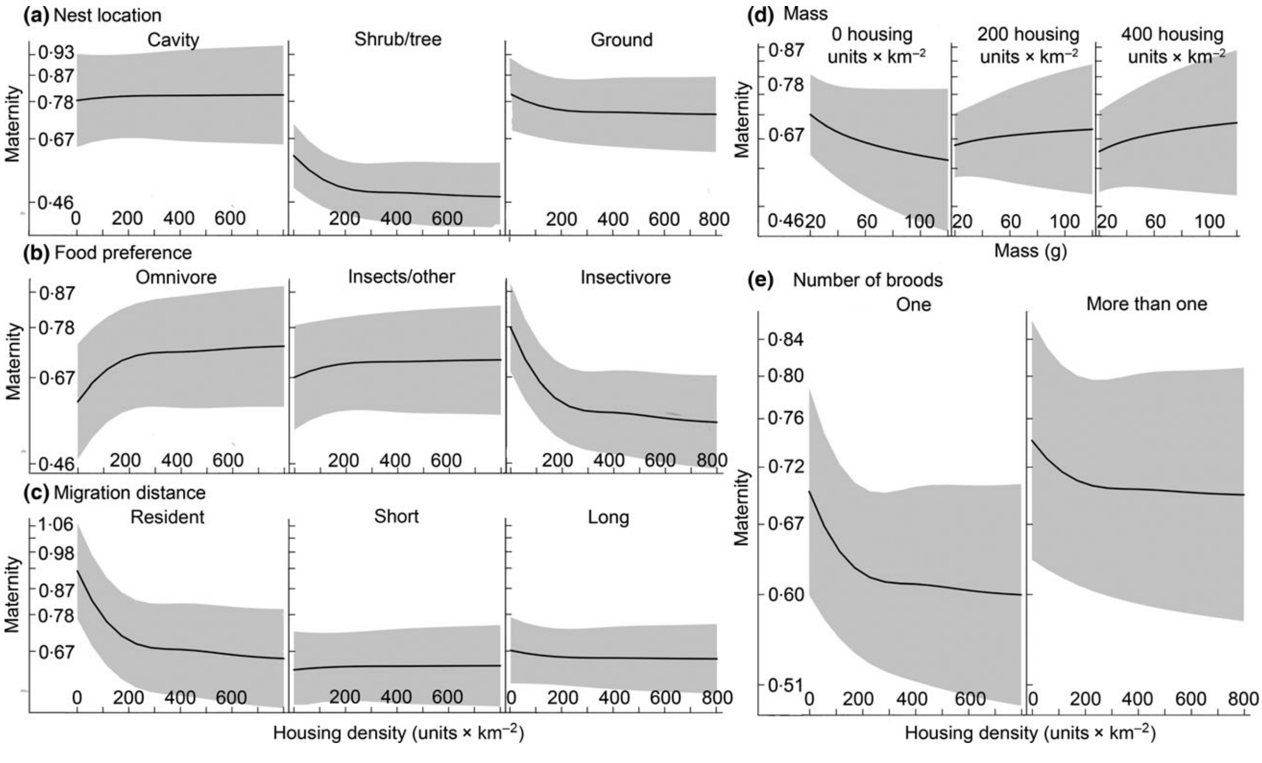

Fig. 2. Back-transformed means and 95% confidence intervals depicting relationship between maternity, our metric for reproduction and housing density for (a) nest location, (b) food preference, (c) migration distance, (d) mass and (e) number of broods.

Had we only evaluated relationships between reproduction or survival and traits in the most urban areas, we might have mistakenly treated differences in demographic rates as direct responses to urbanization, and falsely confirmed many of our hypotheses. For example, we found that residents had greater reproductive success than migrants, so we might have concluded that they respond positively to urbanization; in fact, the trend was negative. Our results demonstrate that conclusions about abundance or vital rates based on species' traits in more urbanized areas should be evaluated relative to baseline values of these parameters (e.g. without considering urban effects; Evans *et al.* 2011). Knowing that some groups of species, for example shrub/tree nesters in our study, have lower baseline survival or reproduction may be useful for assessing which species are at greater risk from potential threats.

We view the fact that some of our expectations were not found, and thus may not have been important in the species studied here, with cautious optimism. Perhaps the natural areas in which the Monitoring Avian Productivity and Survival (MAPS) sites are located are large enough to shield some species from otherwise negative effects of increasing urbanization. It is well known that urban forests are important for both resident and migrant bird species, with area being an important predictor of species presence and abundance (e.g. Fernández-Juricic 2000; Donnelly & Marzluff 2004; Watson, Whittaker & Freudenberger 2005; Sandström, Angelstam & Mikusiński 2006). The MAPS sites are a minimum of 20 hectares, often surrounded by larger natural areas beyond where mist nets for capturing birds are placed. For the species in our study, these sites likely provide some buffer from negative effects of human disturbance, and their protection in urbanizing areas is important for maintaining a diversity of viable species (Pautasso *et al.* 2011). Nevertheless, additional factors should be considered in future research. For instance, our predictions were largely based on studies evaluating variation in abundance, but we did not consider behavioural influences, such as competition between individuals, that may influence local abundance measures more than strict measures of survival or reproduction (Shochat *et al.* 2006). Further, we chose housing density because it has been informative in previous avian studies (Pidgeon *et al.* 2007) and was correlated with other metrics of urbanization (e.g. population density), but metrics such as noise levels or the extent of fragmentation may provide additional insights into why species with specific traits are declining.

The ability to predict how species' respond to urbanization based on shared characteristics is ideal for developing the most efficient strategies to manage species, such as protecting or providing breeding sites or augmenting food sources (Lepczyk, Mertig & Liu 2004b; Robb *et al.* 2008; Balogh, Ryder & Marra 2011). We found relationships between species' traits, urbanization and demographic parameters that suggest it may be possible to make some broad generalizations about species' responses to urbanization. However, these should be confirmed across multiple metrics and may differ across taxa and geographic regions. Our study is one of few with ample data to even attempt to investigate the relationship between traits and demographic rates. While our results affirm some hypotheses based on previous research, we caution against negating relationships that were not found. The availability of long-term data sets is improving our ability to understand species' responses to urbanization, and continued collection of such data should be a research priority. These data are essential for understanding the processes driving observed patterns of species' abundance and for making effective management decisions in an increasingly urban world.

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Data accessibility

Raw data are property of and archived by the Institute for Bird Populations (IBP), P.O. Box 1346, Point Reyes Station, CA 94956-1346, USA. Some parameter estimates can be obtained at http://www.vitalratesofnorthamericanlandbirds.org. Raw data can be obtained by directly contacting Danielle Kaschube, MAPS Coordinator, at dkaschube@birdpop.org. Parameter estimates and covariates used for regression analyses in this manuscript have been uploaded to the Dryad Digital Repository doi:10.5061/dryad.m3d4d (Brown & Graham 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Phylogenetic tree of 68 focal species.

Table S1. Species' characteristics used as predictor variables in models.

Table S2. Coefficient estimates for full models predicting survival and reproduction using the 'MCMCglmm' vs. 'lme4' packages in R.