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ATTITUDES AND ACTIONS TOWARD BIRDS IN URBAN AREAS: HUMAN CULTURAL DIFFERENCES INFLUENCE BIRD BEHAVIOR

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ABSTRACT.—Humans profoundly affect wildlife through environmental modification but they can also influence wildlife through direct interactions. We surveyed human attitudes and actions towards birds in two urban areas (Seattle, Washington, and Berlin, Germany) to determine whether encouraging (e.g., providing bird feeders) and discouraging (e.g., actively repelling) behavior directed at birds affected bird behavior. We studied human and bird behavior across an urbanization gradient (heavy to light urbanization) in both cities to capture variation in urban cover, human density, attitudes, and actions as well as variation in human culture and socioeconomic condition and education. We found that residents of Berlin encouraged birds more than residents of Seattle did, and that Seattleites discouraged birds more than Berliners. These differences varied across the urbanization gradient. Likewise, birds (crows and other songbirds) varied their flight initiation distance across the urbanization gradient, with distances increasing from urban to rural sites. However, in rural sites in Seattle, American Crows (*Corvus brachyrhynchos*) and European Starlings (*Sturnus vulgaris*) had exaggerated flight initiation distances compared with those of American Robins (*Turdus migratorius*) in Seattle and those of Hooded Crows (*C. cornix*), House Sparrows (*Passer domesticus*), and European Starlings in rural Berlin. This exaggerated wariness of humans in crows and starlings is correlated with the relatively high levels of discouraging behavior toward birds by humans in these rural areas in Seattle. These results demonstrate that in addition to habituation to human disturbance, human behavior directed at birds can affect certain species' behavior. *Received 1 June 2011, accepted 31 October 2011.*

Key words: corvids, *Corvus brachyrhynchos*, *C. cornix*, flight initiation distance, human behavior, *Passer domesticus*, *Sturnus vulgaris*, supplemental feeding, *Turdus migratorius.*

Attitudes et actions envers les oiseaux dans les zones urbaines: les différences culturelles des humains influencent le comportement des oiseaux

RÉSUMÉ.—Les êtres humains, par leur modification d'environnement, affectent très profondément la vie des animaux sauvages; mais ils peuvent aussi influencer les animaux sauvages par leur interaction directe. Nous avons étudié les attitudes et les actions des humains vers les oiseaux dans deux localités urbaines (Seattle, Washington and Berlin, Germany) pour déterminer si des encouragements (par exemple, en fournissant des alimenteurs d'oiseau) ou des découragements (repoussement actif) envers les oiseaux, peuvent affecter leur comportement. Nous avons étudié le comportement des humains et des oiseaux parmi un gradient d'urbanisation (de dense à peu peuplé) dans les deux villes, afin de capturer les variations dans le couvrent urbain, densité humaine, attitudes et actions, aussi comme les variation culturelles, les conditions social-économiques et leur éducation. On a remarqué que les résidents de Berlin favorisaient les oiseaux plus que les résidents de Seattle, et que les gens de Seattle décourageaient les oiseaux plus que les gens de Berlin. Ces différences varient parmi le gradient d'urbanisation. De même, les oiseaux (corbeaux et autres oiseaux chanteurs) variaient la distance de leur vol initial parmi le gradient d'urbanisation, avec augmentation de distance de zone urbaine à rurale. Cependant, dans les zones rurales de Seattle, les *Corvus brachyrhynchos* et les *Stornus vulgaris* avait des initiation de vol de distance exagérées comparé à ceux des *Turdus migratorius* à Seattle et des *C. cornix*, des *Passer domesticus* et des *S. vulgaris* dans la zone rurale de Berlin. Cette méfiance exagérée des *C. brachyrhynchos* et des *S. vulgaris* pour les humains est corrélative de l'haut comportement de découragement des humains envers les oiseaux dans ces zones rurales de Seattle. Ces résultats démontrent que, en plus de l'accoutumance au dérangement humain, le comportement humain envers les oiseaux peut affecter le comportement de l'espèce.

THE INFLUENCE OF humans on other animals is profound. Humans affect ecosystems by changing land cover, using resources, producing waste, and changing native communities of fauna and flora (Marzluff et al. 2001, Liu et al. 2007). In particular, urbanization affects species survival, population structure, reproduction, and behavior. As urbanization increases and

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expands worldwide, an understanding of how animals respond to the conversion of wild, rural areas to human-dominated landscapes is necessary to successfully conserve biodiversity. These modifications in land cover also provide a natural experiment for exploring how animals respond to modified environments. Thus, urbanization provides a unique venue for applied and basic theoretical research on natural selection. Birds are particularly well suited for such study in that they are ubiquitous worldwide and responsive (both positively and negatively) to human action (Marzluff et al. 2001, 2005; Chamberlain et al. 2004; Chace and Walsh 2006; Robb et al. 2008; Evans et al. 2009; Clucas et al. 2011).

The major human factors that negatively affect bird species are habitat alteration (removing, fracturing, and changing vegetation) and introduced species (predators, including domestic pets, and competitors; Chace and Walsh 2006). These factors, however, are mostly indirect (i.e., the human actions are not aimed at the birds themselves). Humans can also have direct negative effects on birds, such as physical disturbance (e.g., approaching; Møller 2008, Schlesinger et al. 2008, Evans et al. 2009) and hunting (Fox and Madsen 1997, Casas et al. 2009). Human visitation to parks and other natural areas can disturb birds' foraging, breeding, and nesting behavior (Chace and Walsh 2006). Typically, birds in urban areas are less sensitive to humans approaching them than birds in rural and natural areas (Cooke 1980, Jerzak 2001, Randler 2008; but see Valcarcel and Fernández-Juricic 2009), the assumption being that birds in urban areas habituate to humans. Nevertheless, humans may still negatively affect birds in urban areas simply by walking near a feeding or nesting area (Campbell 2006, Møller 2008).

Humans also can have a positive effect on birds. For example, humans provide supplementary resources in urban areas through direct (bird feeders) and indirect (e.g., garbage) supplementary feeding. In fact, up to 43% of households in the United States and 75% in the United Kingdom feed birds (Robb et al. 2008), and 48% of urban households in the United Kingdom provide food for birds (Evans et al. 2009). The effect of supplementary feeding on birds in urban areas has the potential to be substantial (Lepczyk et al. 2004, Chace and Walsh 2006, Fuller et al. 2008, Robb et al. 2008, Chamberlain et al. 2004). Planted vegetation, buildings, structures, birdhouses, and bird baths also provide novel nesting sites and water sources. Positive effects include increased winter survival, larger population sizes, and, for raptors, a greater prey base (Grubb and Cimprich 1990, Chace and Walsh 2006). Most studies on supplemental feeding have been conducted in rural areas (see Evans et al. 2009); nevertheless, feeding of birds is also common in urban areas. It is not known whether intentional feeding by humans influences birds' wariness of humans.

We tested whether human attitudes and actions affect bird behavior across an urbanization gradient and between two cities: Berlin, Germany, and Seattle, Washington. In a recent survey, we asked residents a range of questions concerning their opinions of birds and about actions directed toward them (Clucas et al. 2011). Specifically, we asked whether they encouraged birds and whether they directed any discouraging behavior toward birds. We defined "encouraging behavior" as providing food to birds (e.g., bird feeders) and "discouraging behavior" as actively repelling birds (e.g., chasing, shooting, and predator decoys). Interactions with animals and attitudes toward them can be influenced by an individual's wildlife knowledge, along with demographic, socioeconomic, and cultural factors. For instance, age, gender, and education can affect whether people feed birds (Lepczyk et al. 2004). In addition, people in deprived areas are less likely to feed birds (e.g., Fuller et al. 2008). Human interest and concern for animals have been shown to vary with age, gender, education level, and knowledge of the animal (see review in Bjerke and Ostdahl 2004, Barney et al. 2005), and people tend to engage in more animal-related activities (e.g., visiting zoos) when they have children (Morgan and Hodgkinson 1999). Cultural differences also exist in human attitudes and actions toward animals, as shown in a survey comparing Germany and the United States (Kellert 1993). Therefore, here we also looked for effects of gender, age, having children, socioeconomic status, education, and culture (Berlin vs. Seattle) on actions toward birds.

To quantify birds' reactions to humans, we measured flight initiation distance (FID), the distance at which a bird initiates fleeing (either by foot or by flight) when approached by a human (Blumstein 2003). We tested birds at the sites associated with human survey data, across the urbanization gradient in both Berlin and Seattle. We tested Hooded Crows (*Corvus cornix*) and House Sparrows (*Passer domesticus*; hereafter "sparrows") in Berlin; American Crows (*C. brachyrhynchos*) and American Robins (*Turdus migratorius*; hereafter "robins") in Seattle; and European Starlings (*Sturnus vulgaris*; hereafter "starlings") in both cities. We selected these species because attitudes toward crows are typically negative whereas attitudes toward charismatic native songbirds are typically positive (Bjerke and Ostdahl 2004). Starlings are native to Berlin, but in Seattle they are an invasive species and considered a nuisance. We examined whether human behavior toward birds (feeding or discouraging) at these sites influenced flight initiation distance. In addition to the typical pattern of increased flight initiation distance from heavy urban to rural areas, we predicted that encouraging or discouraging behavior by humans would decrease or increase flight initiation distances, respectively, if birds adjust their behavior to human behavior.

Methods

Study areas.—The area of Seattle, Washington (47°36′35″N, 122°19′59″W), was originally settled by persons of European descent around 1850, and in 1889 Washington was declared a state. The population around that time was 80,671 (Dryden 1968). Recently the Seattle metro area had a population of 3,275,847 (U.S. Census Bureau 2000).

The area of Berlin, Germany (52°30′2″N, 13°23′56″E), was originally settled by Slavic tribes around 720. Founded in 1244, the city of Berlin had ~8,000 inhabitants by 1400 and 55,000 by 1709 (Taylor 1997). The current population of the Berlin metro area is 3,443,000 (Amt für Statistik Berlin-Brandenburg 2010).

Study sites.—In each city, we selected two study sites at each of four levels of the urbanization gradient (defined by land cover, housing type, and average human density): (1) urban (city center, apartments, 252 ± 143 [average residents hectare^{-1} ± SD]); (2) dense suburban (detached family housing, 46 ± 23); (3) light suburban (detached family housing, 24 ± 17); and (4) rural (villages, farms, detached family housing, 8.5 ± 5); thus, we had a total of four sites at each level and eight sites per city (Fig. 1; for further

FIG. 1. Photographs of the 16 study sites in (left) Seattle, Washington, and (right) Berlin, Germany. The four study sites in each urban gradient type are displayed from top to bottom row: urban, dense suburban, light suburban, and rural (photo credits: Seattle: Jacob Clifford; Berlin: Helena Franke).

details of study sites, see Clucas et al. 2011; for more information about urbanization gradients, see Marzluff et al. 2001).

Human surveys.—We surveyed humans in Berlin from August to December 2008 and in Seattle from October 2009 to February 2010. We attempted to conduct ~30 personal, door-to-door interviews at each site. To notify residents, we posted flyers in mailboxes or in public places about a week before surveying. At the beginning of each interview, residents were briefly told about the focus of the survey (interactions between humans and birds, both positive and negative) and that no specific knowledge of birds was necessary (for further details regarding the human survey, including the complete survey instrument, see Clucas et al. 2011).

Here, we use data from two sections of the survey: (1) general attitude and actions toward birds, specifically whether residents encourage birds ("Do you provide food for birds?") or discourage birds ("Do you do use methods to discourage birds from your home or yard?"); and (2) demographic information (gender, age, have children [yes or no], housing status [rent or own], education level, and annual income level). Berlin income data was converted from Euros to U.S. dollars using the conversion rate from November 2010.

Flight initiation distance.—We tested American Crows and robins in Seattle, Hooded Crows and sparrows in Berlin, and starlings in both cities. Making behavioral comparisons of species across continents has previously been done (e.g., Martin and Clobert 1996). Although these species vary in their relatedness between cities, for our purposes here they fall into similar functional groups: American Crows and Hooded Crows are large birds that are generally disliked by humans and thought a nuisance (Clucas et al. 2011), whereas robins and sparrows are smaller native birds that are generally liked by humans and thought charismatic (Bjerke and Ostdahl 2004). Starlings are a native species in Germany and a generally valued species; however, in the United States they are generally disliked and thought a nuisance. Therefore, we selected these species in part because of typical differences in human attitudes toward them, as well as because they occur across the urbanization gradient on all eight study sites in their respective cities.

We collected flight initiation distance data during the breeding seasons (March–June: Berlin, 2009; Seattle, 2010) but before the nestling or fledgling stage, because crows can become aggressive during these stages (Knight et al. 1987, B. Clucas and J. M. Marzluff pers. obs.). In each city, we used the same eight study sites where the human surveys were conducted (see above). Data were collected between 0700 and 1700 hours by two observers. We measured FID using the following methods: once a bird was spotted on the ground, the starting distance (distance between the bird and the observers) was recorded by the first observer with a laser rangefinder (Leica Rangemaster CRF 900), and then the second observer began walking directly at the bird at a steady pace, looking directly at the bird. Once the bird initiated fleeing, the second observer stopped and the distance walked was subtracted from the starting distance to give the FID. We recorded the escape behavior (flew, hopped or ran, or walked away), the number of conspecifics in a 10-m radius, distance to cover (using the rangefinder), as well as temperature, wind speed, and light level using a 4-in-1 Environment Meter (LT Lutron, LM-8000). Because bird size is known to affect its flight initiation distance (see Blumstein 2006), we also included this variable in our analyses (crow species were categorized as large; sparrows, robins, and starlings as small).

Statistical analyses.—We analyzed the human survey data using a combination of chi-square and Mann-Whitney tests for the demographic data (due to non-normal data). We used logistic regression to examine what factors influenced human behavior. Feeding and discouraging birds were split into four percentage categories based on natural distributions determined by histograms.

A general linear model (GLM) was used to test whether survey and environmental factors had an effect on flight initiation distance as follows: urban gradient, starting distance, distance to cover, number of conspecifics, and wind, light and temperature were entered as covariates; and species, discouraging category level, encouraging (feeding) category level, and bird size were entered as fixed factors. In order to test for homogeneity of regression slopes, we ran an analysis of covariance (ANCOVA) with a customized model that included all interaction terms possible with all the covariates to determine whether any of these covariate interaction terms were significant.

We also ran a general linear mixed model (GLMM) that included study site nested within city as a random factor to test for and eliminate the possibility that our site selections along the urban gradient in each city were not representative of other locations in Berlin and Seattle.

Finally, we removed any possible variation in flight initiation distance due to escape strategy used by birds (flying vs. fleeing on foot; Rodriguez-Prieto et al. 2008) by rerunning the analysis with only cases in which birds flew immediately. All analyses were conducted using PASW, version 18.0 (SPSS, Chicago, Illinois).

RESULTS

Human surveys.—We surveyed 209 residents in Seattle and 356 residents in Berlin. There were no significant differences in the numbers of males and females surveyed in either city, but the age structure of Berlin residents was skewed slightly older than that of Seattle residents (mean ± SE: Seattle: 49.6 ± 1.97 years, Berlin: 54.5 ± 0.96; ANOVA: $F = 9.90$, df = 1 and 563, $P = 0.002$). Seattle residents had significantly more years of education (15.3 ± 0.11) than those in Berlin (12.6 ± 0.21; Mann-Whitney test: $U = 16570.5$, $P < 0.0001$, $r = -0.484$) and a higher annual income level (Seattle median: $75,000–100,000; Berlin median: $16,250–24,300; Mann-Whitney test: $U = 9007.5$, $P < 0.0001$, $r = -0.23$). Seattleites were also more likely to own homes (78%) than Berliners (55%; $\chi^2 = 28.72$, df = 1, $P < 0.0001$).

Whether residents fed birds was influenced by several factors: city, location on urbanization gradient, age of respondent, and the interaction between home ownership and having children (Table 1). First, Berliners fed birds slightly, although significantly, more than Seattleites (in particular in dense suburban sites; Fig. 2). Second, respondents living in urban sites fed birds less than those living in suburban to rural sites (Fig. 2). Third, older respondents were more likely to provide food for birds than were younger respondents. Finally, homeowners fed birds more often than renters, but both homeowners and renters with children fed birds more than homeowners and renters without children (32.8% and 8.3% vs. 5.5% and 3.9%, respectively). There were no significant effects of gender, years of education, or income level on bird feeding behavior for either city, so these variables were subsequently removed from the model.

We asked whether survey participants used any methods to discourage birds from their homes or yards. In Berlin, residents reported using several tactics: physical barriers (1.6%; e.g., putting up nets over balconies or ponds), chasing or hand-clapping (4.8%), yelling at birds (0.5%), and using predator decoys to scare birds (1.4%). In Seattle, residents reported using physical barriers (3.3%; putting up nets over ponds or putting spikes on housing), using predator decoys to scare birds (1.0%), throwing objects at and chasing birds (4.8%), setting off bottle rockets to scare birds (0.5%), and shooting birds (3.8%; with the intent of lethal harm). Rates of discouraging behavior differed between cities, across the urbanization gradient (Fig. 3), with age of respondent and with their home ownership status (Table 2). Residents were more likely to discourage birds if they lived in Seattle, were older, and owned

Table 1. Factors that influenced feeding of birds by survey respondents in Seattle and Berlin (logistic regression; asterisks indicate significant factors).

	B	SE	Wald statistic	df	*P*	Exp (*B*)
City*	0.463	0.208	4.972	1	0.026	1.589
Urban gradient*	–0.184	0.044	17.019	1	0.000	0.832
Age of respondent*	0.027	0.006	18.291	1	0.000	1.027
Ownership of residence	0.076	0.285	0.071	1	0.790	1.079
Has child(ren)	0.008	0.312	0.001	1	0.978	1.009
Has child(ren) by ownership of residence*	–1.225	0.456	7.211	1	0.007	0.294
Constant	–0.677	0.398	2.895	1	0.089	0.508

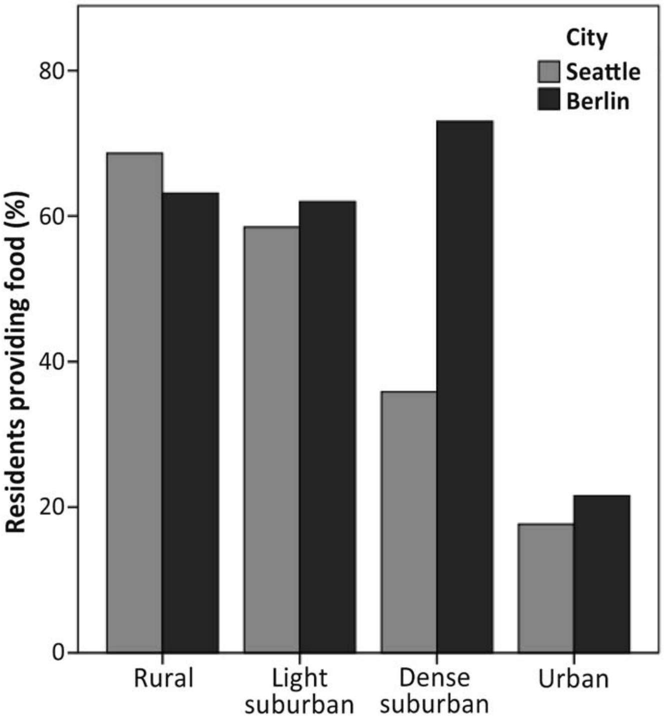

FIG. 2. Percentages of survey respondents who feed birds across the urbanization gradient in Seattle and Berlin.

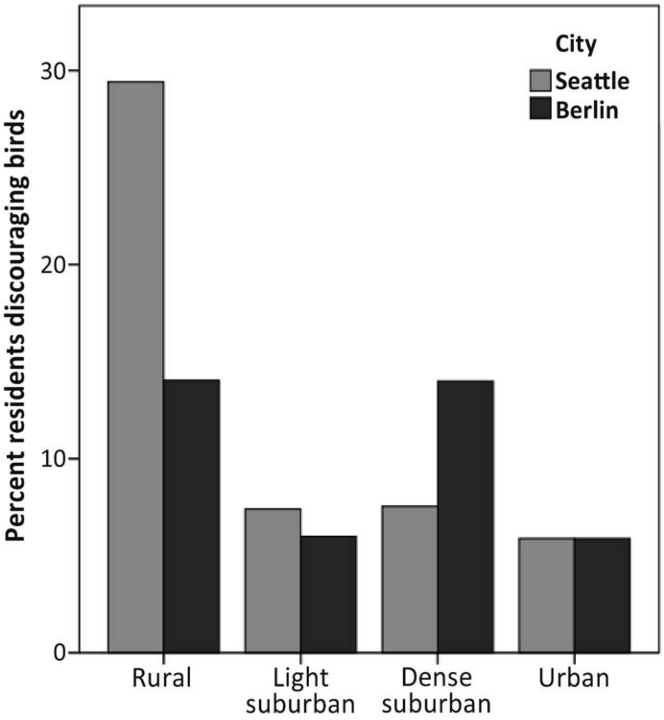

FIG. 3. Percentages of survey respondents who discourage birds across the urbanization gradient in Seattle and Berlin.

their homes. However, there was a significant interaction between city and urbanization gradient: residents in rural areas in Seattle were much more likely to discourage birds than residents in suburban to urban areas, but Berlin residents were equally likely to engage in minimal amounts of discouraging behavior across the urbanization gradient (Table 2 and Fig. 3). We found no effect of gender, years of education, or annual income level on discouraging behavior.

In the rural areas in Seattle, most of the discouraging behavior was directed at crows (60%) and the rest at starlings (20%) and other bird species (Great Blue Heron [*Ardea herodias*] and woodpeckers [Picidae], 20%). All reports of shooting birds were from the rural sites, and the target species were always crows or starlings.

Flight initiation distance.—We attempted to obtain observations of 15 individuals per species at each of the four levels of urbanization. We achieved this for all species (average per level: 22.6) except starlings (average per level: Berlin: 4.5, Seattle: 7). Therefore, because of the small sample sizes for the starlings and subsequent unequal variances if included in the main model, we analyzed this species separately.

In the main general linear model, flight initiation distance was influenced by several factors (Table 3). First, the covariates "starting distance" and "distance to cover" were significantly correlated with flight initiation distance (Table 3). Like Blumstein (2003), we found that the farther away from the bird the human observer started and the farther from cover the bird was, the larger the flight initiation distance. We also found that the covariate "urbanization gradient" had an effect on flight initiation distance, in that birds' wariness of humans increased from urban to rural sites (Table 3 and Fig. 4). Discouraging behavior toward birds also had an effect on flight initiation distance; however, this influence depended on species (Table 3). American Crows (in Seattle) had exaggeratedly long flight initiation distances at sites where humans discouraged them most (Fig. 5). This relationship did not exist for

TABLE 2. Factors that influenced survey respondents' discouraging of birds in Seattle and Berlin (logistic regression; asterisks indicate significant factors).

	B	SE	Wald statistic	df	*P*	Exp (*B*)
City*	–1.357	0.565	5.762	1	0.016	0.257
Urban gradient*	–0.304	0.112	7.341	1	0.007	0.738
Age of resident*	0.018	0.009	4.138	1	0.042	1.018
Ownership of residence*	–0.820	0.417	3.876	1	0.049	0.440
City by urban gradient*	0.324	0.141	5.264	1	0.022	1.383
Constant	–1.749	0.608	8.284	1	0.004	0.174

TABLE 3. Factors that influenced flight initiation distance in our study (general liner model: univariate analysis of variance).

Source	Type III sum of squares	df	Mean square	*F*	*P*
Corrected model	18,460.48	12	1,538.37	38.468	0.000
Intercept	1,939.36	1	1,939.36	48.495	0.000
Starting distance	1,841.61	1	1,841.61	46.050	0.000
Urban gradient	1,025.47	1	1,025.47	25.642	0.000
Distance to cover	317.23	1	317.23	7.933	0.005
Species	785.67	3	261.89	6.549	0.000
Discourage level	1,804.53	3	601.51	15.041	0.000
Species by discourage level	1,557.11	3	519.04	12.979	0.000
Error	13,956.88	349	39.99		
Total	68,751.49	362			
Corrected total	32,417.37	361			

any species in Berlin or for robins in Seattle (Fig. 5). The GLMM with study sites nested within city as a random variable yielded similar results (Appendix 1 in supplementary online material; see Acknowledgments). Number of conspecifics, temperature, light level, maximum wind speed, level of feeding behavior by humans, and bird size (small or large) did not have a significant influence on flight initiation distance and were not used in the final model.

The ANCOVA including all interactions among factors and covariates showed that none of these interactions was significant ($P > 0.05$), indicating that starting distance, distance to cover, and urban gradient all had similar relationships with all of the species and levels of discouraging behavior (and that the assumption of homogeneity of slopes was met for these variables).

The birds' initial escape behavior was predominantly flying away (79.8%) and, less frequently, running or hopping (11%) or walking (9.4%), and we found the same results as the GLM above for an analysis of flight initiation distance limited to immediate flying behavior (see Appendix 2 in supplementary online material).

Starting distance, urbanization level, and the interaction of discouragement level and city significantly affected flight initiation distance in starlings (GLM: starting distance: $F = 24.043$, df = 1 and 39, $P < 0.0001$; urbanization level: $F = 4.489$, df = 1 and 39, $P = 0.041$; discouragement level × city: $F = 3.063$, df = 3 and 39, $P = 0.039$). Number of conspecifics, temperature, light level,

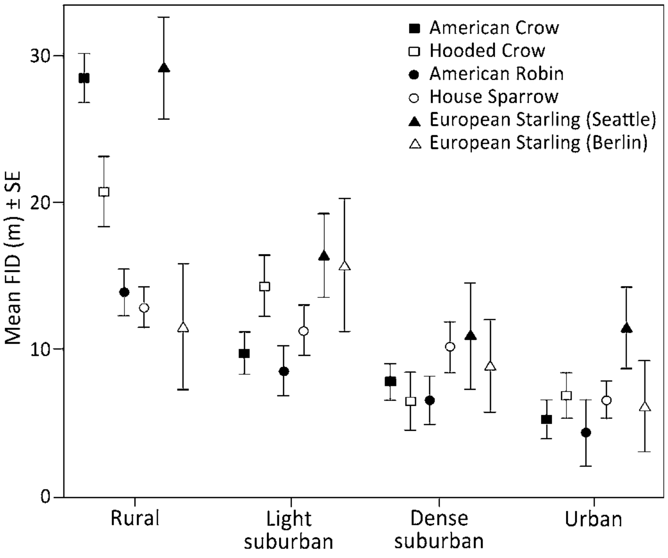

FIG. 4. Mean flight initiation distance of bird species in Seattle (filled symbols) and Berlin (open symbols) across the urbanization gradient. Means and standard errors for crows, sparrows, and robins were estimated from a general linear model with covariates of starting distance = 30.1 m and distance to cover = 9.6 m. Means and standard errors for starlings were estimated from a general linear model with covariates of starting distance = 30.8 m.

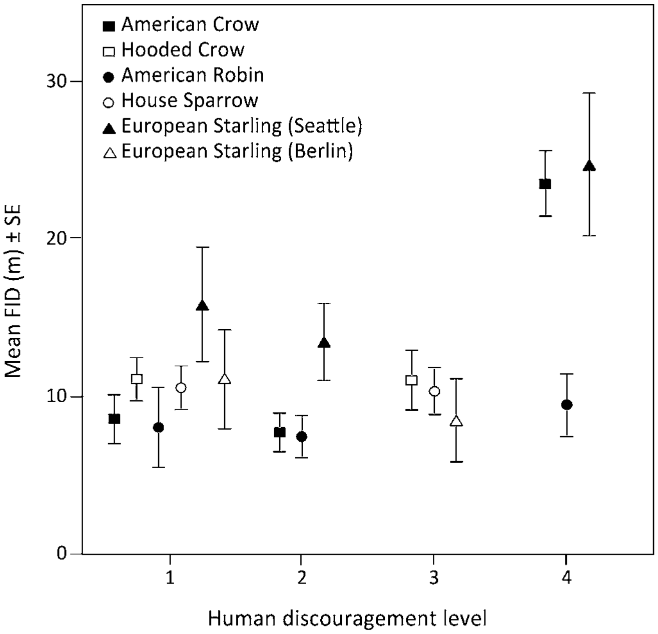

FIG. 5. Relationship between discouraging behavior directed at birds by humans and flight initiation distance in Seattle (open symbols) and Berlin (filled symbols). Means and standard errors for crows, sparrows, and robins were estimated from a general linear model with covariates of starting distance = 30.1 m, distance to cover = 9.6 m, and urbanization level = 2.6. Means and standard errors for starlings were estimated from a general linear model with covariates of starting distance = 30.8 m and urbanization level = 2.6. Discouragement levels are 1 = 5–6%, 2 = 7–8%, 3 = 14–15%, and 4 = 29–30%.

maximum wind speed, level of feeding, and distance to cover did not have a significant effect on flight initiation distance. Similar to crows in Seattle, starlings in Seattle had a much longer flight distance in rural areas where human discouragement of birds was relatively high, whereas such a pattern did not exist for starlings in Berlin (Figs. 4 and 5). However, these results should be viewed with caution because of relatively small sample sizes. Starlings flew the majority of the time (Berlin: 77.8%, Seattle: 78.6%), but an analysis including only immediate flying escape behavior was not possible for this species because the sample sizes in certain discouragement levels were too small for this limited data set.

Discussion

We found that discouraging behavior directed at birds influenced bird flight initiation distances; depending on species and city, birds had a longer flight distance in areas with the highest frequency of discouraging behavior. In Seattle, there was an exaggerated level of discouraging behavior in rural areas, which could explain why American Crows are so wary of humans in these areas compared with robins in the same areas and compared with Hooded Crows and sparrows in rural areas in Berlin. Similarly, when comparing starlings between the two cities, their wariness of humans was exaggerated in rural areas in Seattle but not in Berlin. Therefore, although flight initiation distance might be negatively correlated with degree of urbanization because of differences in density of humans (and, thus, differences in probability of experiencing human traffic), we showed that American Crows and starlings in Seattle might also be responding to differences in human behavior toward birds.

It is possible that the difference between Berlin and Seattle in length of time since urbanization began might affect bird behavior toward humans (Martin and Clobert 1996), and therefore we might expect American species to be more wary of humans than Berlin species. However, in general our results do not indicate this. All species had similar flight distances in urban sites, and Berlin species even had slightly longer flight initiation distances in light suburban areas compared with Seattle species. We would also expect robins to have a greater wariness of humans in rural areas than Hooded Crows and sparrows, but this was not the case. However, tests with a greater number of species while controlling for phylogenetic relationships would be necessary to further address expected differences in flight initiation distances due to time since urbanization.

We also did not find the expected effect of size on flight initiation distance (see Blumstein 2006), but several factors could explain this. First, our "large" birds were both corvids, which have a large brain size in relation to body size. Large brain size is known to correlate with innovation and intelligence, which may enable crows to more readily adjust to novel environments (Sol et al. 2002) and decrease their wariness of humans compared with other bird species their size. Second, if looking only at our rural data on flight initiation distances, there is a size difference (crows have a longer flight distance than sparrows and robins); however, this difference is not found in suburban or urban areas. Therefore, this reinforces the importance of taking into account the level of human presence when estimating flight initiation distances for bird species.

In general, the differences we found in flight initiation distances between urban and rural areas were similar to those reported in studies in other cities in Germany and Europe (Cooke 1980, Jerzak 2001, Møller 2008, Randler 2008) and in North America (Kennedy and Knight 1992). In addition, two separate studies on other corvid species, the American Black-billed Magpie (*Pica hudsonia*) and the European Magpie (*P. pica*), appear to show a similar pattern as our results regarding influence of human discouragement. Black-billed Magpies subject to persecution in rural areas of Colorado had much longer flight initiation distances (mean: 64.7 m) than in an urban area (9.4 m) in Fort Collins (Kennedy and Knight 1992). European Magpies in Poland also have longer flight initiation distances in rural (36.3 m) than in urban areas (6.4 m; Ochla and Zielona Gora, respectively; Jerzak 2001), but the difference is not as large as in Colorado (Kennedy and Knight 1992). The exaggerated flight initiation distance in rural Colorado areas compared with those in Poland is likely due to the higher frequency of persecution by humans in rural Colorado. Furthermore, Kennedy and Knight (1992) showed that Black-billed Magpies had shorter flight distances in rural areas where they were not persecuted than in areas where they were persecuted (28.9 vs. 64.7 m). These data and our own results suggest that in certain rural areas it is a combination of lower human density (and, thus, less habituation to humans) and human discouragement behavior that increases birds' wariness of humans in comparison with urban areas.

Corvids are exceptionally intelligent (Emery and Clayton 2004, Marzluff and Angell 2005) and have been shown to use tools (Hunt 1996) and many innovative behaviors (e.g., Nihei and Higuchi 2001). Corvids also have amazing memory skills, as shown by jays and nutcrackers (Balda and Kamil 1989). Recently, Marzluff et al. (2010) demonstrated that American Crows can recognize and remember human faces. Crows given a negative experience by a masked human (being trapped) were shown to later mob humans wearing the mask, even months later. Such learning of human individuals may also occur when humans discourage crows from their homes and yards (e.g., shoot at, scare with loud noises). Our results, however, suggest that crows may also generalize across humans. In our experiments and those done elsewhere (e.g., Knight et al. 1987), dangerous individuals did not approach crows, yet crows adjusted their response depending on the general actions of the human population in the area. Crows in rural areas where persecution occurs may thus use a general rule of avoiding any human. Indeed, in our study and others (e.g., Knight et al. 1987), the crows had no previous experience with the specific individuals who conducted the measurements of flight initiation distance.

Can reactions to an approaching human be viewed as an adaptive antipredator response (Frid and Dill 2002)? At the very least, the reaction of nonhuman animals to humans approaching them could be considered a fear response to the disturbance (Stankowich and Blumstein 2005). The degree of selection on behavior may differ depending on whether humans are viewed as a disturbance or a predation threat with lethal consequences. Human hunting has been shown to affect antipredator behavior in prey species. For example, primates adjust their antipredator behavior in areas where they are hunted, compared with protected or no-hunting areas (Croes et al. 2007), and it has been suggested that these adjustments are learned in some species (Bshary 2001).

Other studies of the effect of hunting on birds have demonstrated behavioral shifts in hunting areas (Fox and Madsen 1997, Casas et al. 2009). Our work shows how human discouragement behavior (not always lethal) can also affect bird behavior; however, it is unknown whether this increased wariness of humans is a learned trait in American Crows or whether selection has created human-wary individuals in rural areas. In either case, such wariness of humans can be quite costly for birds because it decreases the amount of time spent on foraging and breeding behavior.

Our survey also demonstrated that humans varied their encouraging behavior across the urbanization gradient in both Seattle and Berlin—people in the city center fed birds less than those in suburban and rural areas. However, Berliners were more likely than Seattleites to feed birds. Flight initiation distance of birds in both cities did not positively correlate with this form of encouraging behavior. This may be explained by several factors. First, it is likely that habituation to humans plays a larger role in how wary birds are of humans (i.e., birds have short flight distances in urban areas where there are more humans). Second, many humans feed birds indirectly by using bird feeders, which may preclude birds' ability to make an association with humans themselves. Nevertheless, providing bird feeders can influence birds at population and community levels by increasing abundance and fitness of certain species and changing the diversity and composition of species present in an area (Fuller et al. 2008, Robb et al. 2008, Clucas et al. 2011).

In the emerging field of urban ecology it is important to understand the mechanisms through which humans affect wildlife populations, communities, and ecosystems (Liu et al. 2007, Shaw et al. 2008). Our study highlights a possible mechanistic link between the behavior of people and animals in urban systems. We found differences in human–avian interactions between a German and North American city across the urbanization gradient. These differences between Berlin and Seattle may be linked to cultural differences in attitudes toward wildlife. Kellert (1993) found that survey respondents from the United States had higher levels of "negativistic" views (indifference, dislike, or fear of animals) and "utilitarian" views (interest in practical value of animals) toward wildlife than Germans, and that Germans had higher levels of "moralistic" and "naturalistic" attitudes (concern for the mistreatment of animals and affection for wildlife or nature, respectively). Kellert's (1993:60) results further showed that Germans "expressed an unusual willingness to sacrifice practical human benefits for the sake of nature and animals." Moreover, Kellert (1993) found that U.S. respondents were more likely to participate in and favorably view hunting of wild animals. The results of our study appear to follow such generalizations, in that Berliners were less likely to discourage birds and more likely to feed them than Seattleites. Additional questions on our survey also showed that respondents from Berlin were more likely to provide nest boxes (Clucas et al. 2011) and held conservation issues at a higher level of importance (B. Clucas unpubl. data). The differences between Berlin and Seattle in humans' discouraging behavior toward birds across the urbanization gradient were reflected in how wary certain species were of humans. This pattern is likely to be replicated across similar gradients of directed discouraging behavior throughout other urban areas and should be considered when dealing with conservation or management of urban species.

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