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Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding

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Anthropogenic changes to the landscape and climate cause novel ecological and evolutionary pressures, leading to potentially dramatic changes in the distribution of biodiversity. Warm winter temperatures can shift species' distributions to regions that were previously uninhabitable. Further, urbanization and supplementary feeding may facilitate range expansions and potentially reduce migration tendency. Here we explore how these factors interact to cause non-uniform effects across a species's range. Using 17 years of data from the citizen science programme Project FeederWatch, we examined the relationships between urbanization, winter temperatures and the availability of supplementary food (i.e. artificial nectar) on the winter range expansion (more than 700 km northward in the past two decades) of Anna's hummingbirds (*Calypte anna*). We found that Anna's hummingbirds have colonized colder locations over time, were more likely to colonize sites with higher housing density and were more likely to visit feeders in the expanded range compared to the historical range. Additionally, their range expansion mirrored a corresponding increase over time in the tendency of people to provide nectar feeders in the expanded range. This work illustrates how humans may alter the distribution and potentially the migratory behaviour of species through landscape and resource modification.

1. Introduction

The increase in temperatures globally has allowed many species to colonize regions that were previously inhospitable [1]. This has led to widespread changes in species' distributions, particularly poleward range shifts [1–8]. Concurrently, urbanization is changing biodiversity in dramatic ways, such as by reducing the number of species in urban areas and shifting the composition towards generalists [9,10]. Climate change and urbanization may interact and lead to non-uniform consequences across a species's range. For example, urban microclimates at range margins may facilitate geographical expansion [11,12] or reduced migratory behaviour [13–16]. This climate-tempering effect of urbanization may be related to the local retention of heat in urban areas ('heat island effect') [17], increased availability of non-native fruit, seeds or flowers that provide food throughout the winter [18], or increased availability of supplementary food (e.g. seed, suet, meat or nectar) [19–21]. Interactions between urbanization and climate change may make both effects even more pronounced and impactful to species' distributions [11,22].

Supplementary feeding is an aspect of urbanization that has the potential to affect both the distribution and behaviour of avian taxa on a broad geographical scale [19–21,23–27]. Up to half of households in the United States, United Kingdom and Australia have been estimated to offer supplementary food to wild birds [28]. The ecological and evolutionary impacts of this widespread hobby are potentially vast; for example, many species show increased reproductive success in response to supplementary food [20,24]. Other potential consequences of supplementary feeding include increased winter survival and decreased migration
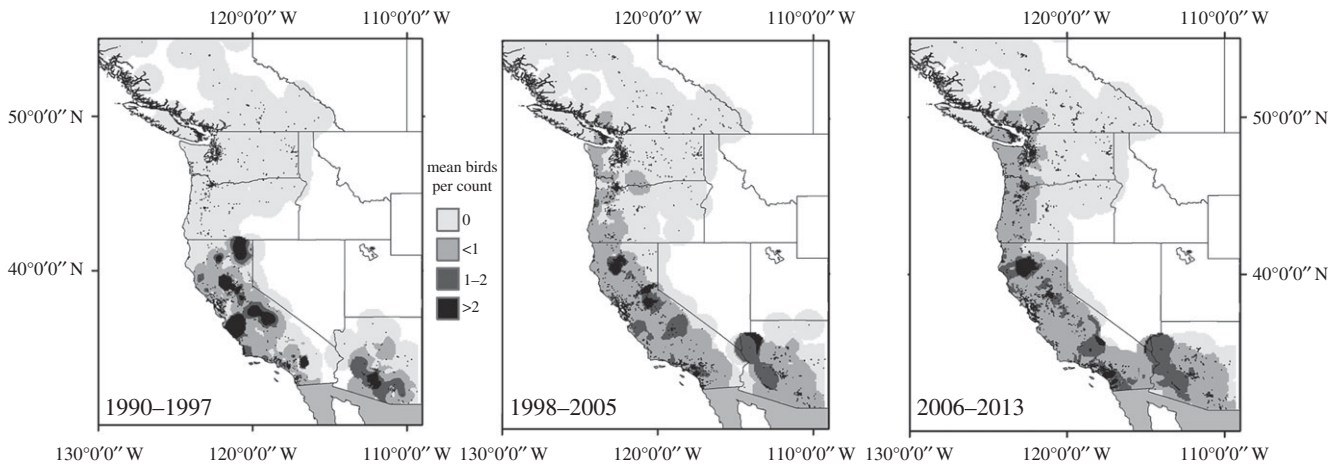
Figure 1. The distribution of Anna's hummingbirds in winter (January and February) at Project FeederWatch count sites (small black dots) over 24 years. Mean maximum birds by site, binned into three time periods: 1990–1997 ($n = 1913$ sites), 1998–2005 ($n = 3583$ sites) and 2006–2013 ($n = 3151$ sites). Maps generated using ArcGIS 10.0, kriging interpolation (ESRI Inc., 1999–2010).

tendency, documented in a few species of birds and even mammals [29–33]. This possible consequence of supplementary feeding has not been explored in nectivorous birds, despite a pattern of northward winter range expansions observed in several North American hummingbirds [34–37].

The Anna's hummingbird (*Calypte anna*) provides a case study in which to investigate the relative contributions of climate, urbanization and supplementary feeding on potential changes in migratory behaviour and resulting shifts in range. This species has shown a significant northward winter range expansion over the past two decades (figure 1) [38–40]. The first record in Alaska was in 1971 [38], and there is now a considerable post-breeding movement northward into Canada and Alaska [41]. Historically, Anna's hummingbirds at the northern limits of their range would move south for winter and return the following spring to breed. Now many individuals overwinter and presumably breed at these northern latitudes, potentially eliminating or shortening their southward movement [40]. Because Anna's hummingbirds are small (5–6 grams) and require reliable, daily access to food to maintain their high metabolism, the northern edge of their winter range is likely to be limited by both temperature and nectar availability [42,43]. The cause of their winter expansion remains speculative, but may be driven by warming winter temperatures, increased urbanization or increased winter supplementary feeding [35].

Here, we quantitatively documented the range expansion of the Anna's hummingbird using an occupancy modelling framework [44] and data from Project FeederWatch, a long-term citizen science programme [45]. We used climate data, urbanization indices and estimates of supplementary feeding prevalence from 1997–2013 to test two alternative hypotheses for explaining their winter range expansion: (i) that the expansion has been facilitated by increased availability of anthropogenically provided habitat or food, or (ii) that the expansion is due solely to warming winter temperatures. Specifically, we predicted that if anthropogenic habitat and food provisioning has facilitated the winter range expansion of Anna's hummingbirds, then (i) hummingbirds should be occurring in areas with lower temperatures than previously occupied, (ii) hummingbirds should be preferentially colonizing areas with higher urbanization in the expanded range, but not in the historical range, and (iii) hummingbirds should be

more dependent upon supplementary food (i.e. nectar feeders) in the expanded range than in the historical range. In contrast, if increasingly mild winters have facilitated the range expansion irrespective of anthropogenic habitat and food, then we predicted that (i) hummingbirds should be occurring in areas with the same climate envelope as previously occupied, even though those areas are now farther north, (ii) hummingbirds should be equally associated with urban locations in the expanded range and the historical range, and (iii) hummingbirds should be equally dependent upon supplementary feeders in the expanded range and the historical range.

2. Methods

(a) Study species

Anna's hummingbirds inhabit the west coast of North America, as far south as northwest Baja California and Mexico, and as far north as southwest British Columbia [35]. They are one of the few species of hummingbirds in North America that are not long-distance migrants, and their local seasonal movements are complex, poorly understood and thought to be related to harshness of weather conditions [35,41]. Nesting occurs between December and June depending upon the latitude, with earlier nesting at lower latitudes. In late summer in southern locations there is a movement to higher elevations following peaks in flower abundance [35]. Birds are commonly found in scrubby or suburban habitat with suitable bushy vegetation and are frequently attracted to yards with nectar feeders and flowering plants [35].

(b) Data sources
(i) Project FeederWatch

Data on Anna's hummingbird occupancy were collected through the citizen science programme Project FeederWatch (PFW), run through the Cornell Laboratory of Ornithology and Bird Studies Canada [45]. PFW participants follow a standardized protocol to count the maximum number of every species seen in the proximity of a bird feeding station during periodic 2-day counts. These counts are repeated as often as every week from November–April each year. By requiring that participants only report the maximum number of each species in view at one time during the count, the protocol ensures that participants are not repeatedly recording the same individual birds within a count. Additionally, participants report all of the species seen, so the protocol allows
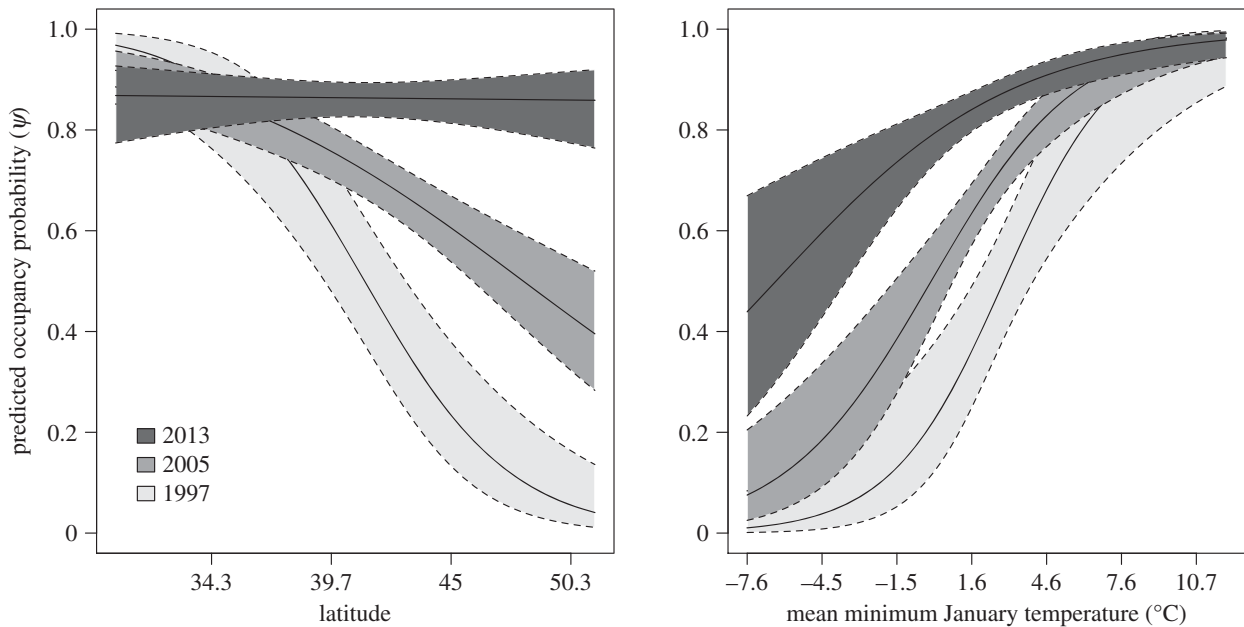
Figure 2. Predicted occupancy probability (ψ) of Anna's hummingbirds as a function of (*a*) latitude and (*b*) minimum January temperature (°C) for 1997 (*n* = 98 sites; light grey), 2005 (*n* = 356 sites; medium grey) and 2013 (*n* = 434 sites; dark grey). 95% CIs are shown. Model results given in table 2.

inference about both presence and absence (detection and non-detection) of species in every count. All participants report an estimate of the amount of time that they watched their feeders (effort) and the date of the observation (date).

We extracted Anna's hummingbird occupancy data from PFW sites in Arizona, California, Oregon and Washington from 1997 to 2013. We restricted all occupancy analyses to sites with nectar feeders because sites offering nectar at some point between November and April were much more likely to have humming-birds than sites without nectar feeders (79% of sites with nectar feeders had a hummingbird compared with only 28% of sites without nectar feeders; likelihood ratio test: $\chi^2_1 = 575.3$, $p < 0.001$, $n = 2306$ sites). We also restricted all occupancy analyses to obser-vations made during the months of December–February so late autumn (November) or early spring (March–April) hummingbird movements would not influence our results.

(ii) Climate and elevation data
We extracted the daily minimum temperature (Tmin), averaged over all days for the month of January (mean minimum January temperature) and the total monthly precipitation (Ppt) for the month of January (total January precipitation) for each site and year, from the PRISM Climate Group gridded dataset (Oregon State University, http://www.prism.oregonstate.edu). We chose January as the representative winter month because that month was temporally central to the bird occupancy data (December–February). To control for the potential effects of topography on occupancy, given that there are known elevational movements of Anna's hummingbirds [35], we extracted elevation data for each site from the CGIAR Consortium for Spatial Information SRTM 90 m Digital Elevation Database (http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1).

(iii) Housing density and land cover data
We calculated housing density, defined as the total number of housing units per area, following methodology in [46]. Housing units were based on a nationwide, spatially explicit dataset at the partial block group level, which corrects for variation introduced into census blocks by political boundaries. Housing units include permanent residences, seasonal houses and vacant units [46].

At each partial block group throughout the conterminous US, housing density was estimated based on the 2000 US decennial census [46], and we used these estimates to characterize housing development throughout our study area. To quantify housing density at each site, we summarized housing density within 1 km circular buffers of each site using the tool 'intersect' in ARCGIS v. 10.1. We used the 1 km radius buffer because this was an approximate home range given for several breeding Anna's hummingbirds [41]. Due to the presence of outliers, we log-transformed the housing density data before analysis.

We extracted the proportion of urban land cover for each site from the 2011 National Landcover Database, with land cover classes 21 (developed, open space), 22 (developed, low intensity), 23 (developed, medium intensity), and 24 (developed, high intensity; http://www.mrlc.gov/nlcd11_leg.php). Within each 1 km circular buffer of each site we divided the total number of cells (30 × 30 m resolution) of the focal urban land cover by the total number of cells within the buffer, which gave us the proportion of urban land cover at each site.

(c) Statistical analysis
We explored the range expansion of Anna's hummingbirds using an occupancy-modelling framework implemented with the R pack-age unmarked [47]. Occupancy models estimate the probability of a focal species occupying a site given imperfect detection [48]. Fol-lowing [11], we used the single-season modelling framework [48] to explore how the relationships between occupancy, latitude and temperature changed over time. Single-season models assume a closed system with no extinction or colonization, which approxi-mates our expectations for a December–February sampling interval. Although mortality and emigration are certainly possible during this (or any) sampling interval, we focused on a time period when the species is largely sedentary. To quantify the northward expansion, we created three single-season models of hummingbird occupancy as a function of latitude for the years 1997 (*n* = 98 sites), 2005 (*n* = 356 sites) and 2013 (*n* = 434 sites) with date and effort as observation covariates. Sample sizes differed across years because of different rates of participation in PFW, but occupancy models are robust to such variation as long as the sampled sites are repre-sentative of the region or time period of interest. We have no reason

Table 1. Single-season model estimates relating Anna's hummingbird occupancy (ψ) to latitude and mean minimum January temperature for 3 years (models estimates correspond to figure 2). Effort and date were included in all models as observation-covariates. p-values < 0.05 are given in italics.

predictor	year (n sites)	estimate	s.e.	z	p
latitude	1997 (98)	−1.64	0.32	−5.21	*0.000*
	2005 (356)	−0.71	0.14	−5.23	*0.000*
	2013 (434)	−0.02	0.15	−0.14	0.891
temperature	1997 (98)	1.33	0.32	4.22	*0.000*
	2005 (356)	1.02	0.18	5.69	*0.000*
	2013 (434)	0.64	0.15	4.27	*0.000*

to suspect that sampled sites were not representative of their respective regions and time periods. To test the prediction that contemporary hummingbirds are occupying sites with lower temperatures than historically occupied, we created three single-season models of hummingbird occupancy as a function of mean minimum January temperature for the same sites and years (1997, 2005 and 2013). Although there are known long-term patterns of warming that have occurred in the Pacific Northwest [49,50], we also tested how the mean minimum January temperature has changed at PFW sites from 1997 to 2013 using a linear mixed model with year as a fixed effect and site ID as a random effect, implemented with the R package lme4. For this analysis we included sites that did not offer nectar feeders because we were not assessing hummingbird occupancy. We binned sites into those from the historical winter range (below 42° latitude, $n = 1269$ sites) and those from the expanded winter range (above 42° latitude, $n = 1037$ sites). We chose this geographical demarcation based on the distribution of hummingbirds in the early years of the study (1990–1997; figure 1).

To test the hypothesis that the winter range expansion was associated with colonization of urban habitats (and potentially provisioning of supplementary food) rather than winter temperatures irrespective of habitat, we used a multi-season modelling framework. Multi-season models allow for both extinction and colonization between seasons and are therefore appropriate for modelling occupancy over a multiple year sampling interval [51]. We used the subset of sites from 2002 to 2013 that offered nectar feeders and for which we had housing density and land-cover data. We omitted years preceding 2002 because of small sample sizes (fewer than 45 sites per year). We binned sites into those from the historical range ($n = 539$ sites) and the expanded range ($n = 366$ sites), and for each region modelled hummingbird colonization as a function of the site covariates: housing density, proportion of urban land cover, elevation, mean minimum January temperature and total January precipitation. Because we wanted to compare all site covariates in a consistent quantitative way, but some covariates were static across years (housing density, proportion of urban land cover and elevation) and some temporally dynamic (temperature and precipitation), we transformed the dynamic variables to static variables by calculating a mean across years. All site covariates were weakly correlated ($r < 0.4$) except housing density and proportion of urban land cover, which were strongly correlated ($r = 0.8$). We included observation effort and date as observation-covariates influencing detection, and latitude as a site covariate influencing occupancy.

In addition to comparing the explanatory power of each site covariate in models with all covariates (global models), we used a model-selection approach with a criterion of $\Delta AIC < 2$ indicating equivalent models to assess the importance of each site covariate on colonization in the historical versus the expanded
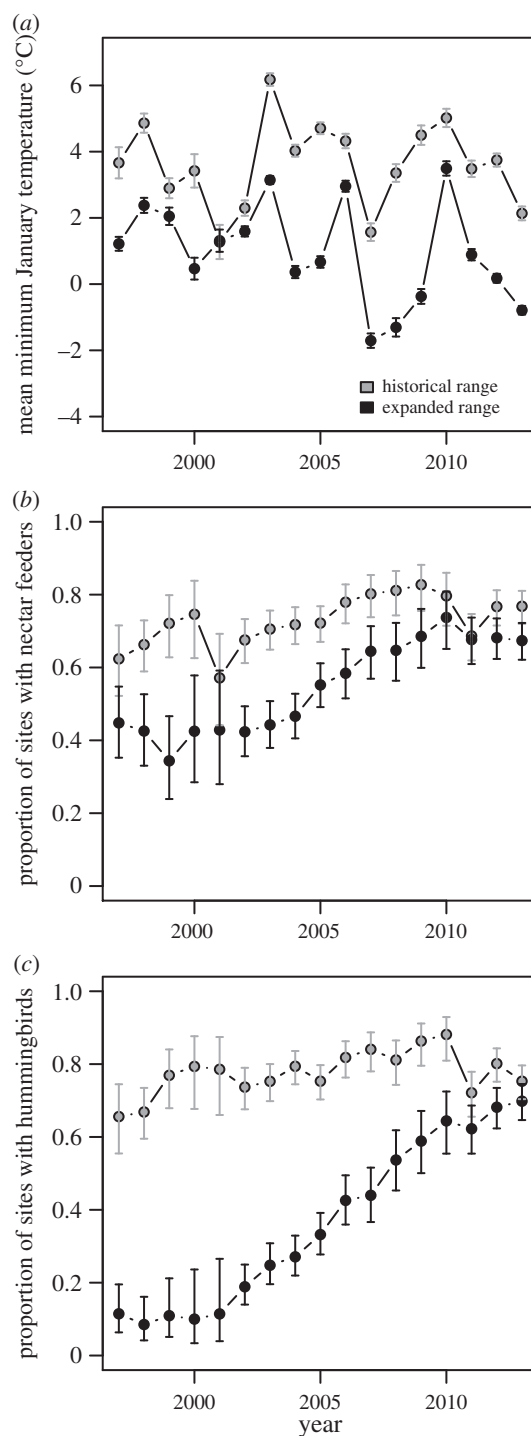

Figure 3. (a) Mean minimum January temperature (°C) from 1997 to 2013 in the historical range (below 42° latitude; grey circles, $n = 1269$ sites for all panels) and the expanded range (above 42° latitude; black circles, $n = 1037$ sites for all panels). Error bars indicate standard error. (b) Proportion of sites offering nectar feeders from 1997 to 2013 in the historical range and the expanded range. Error bars indicate binomial standard error. (c) Proportion of sites supporting Anna's hummingbirds from 1997 to 2013 in the historical range and the expanded range. Error bars indicate binomial standard error.

range. We compared models with all but one of each site covariate, univariate models with only one of each site covariate, the putative best models for each region (for the historical range, the univariate model with elevation as the site covariate and for the expanded range, a model with housing density and temperature as the site covariates), the global model, and a null model with no site covariates. All models converged and produced reasonable estimates and standard errors. Null models had low

Table 2. Multi-season model estimates for years 2002–2013 relating Anna's hummingbird colonization (γ) to all site covariates ('predictor') in the historical range and the expanded range. Effort and date were included in each model as predictors of detection (p) and latitude as a predictor of occupancy (ψ). p-values < 0.05 are given in italics.

location	predictor	parameter	estimate	s.e.	z	p
expanded range (above 42°)	effort	p	0.02	0.04	0.44	0.657
$n = 366$ sites	date	p	−0.22	0.04	−5.82	*0.000*
	latitude	ψ	−0.75	0.22	−3.42	*0.001*
	proportion urban	γ	−0.13	0.18	−0.73	0.467
	elevation	γ	0.01	0.21	0.04	0.965
	housing density	γ	0.73	0.20	3.57	*0.000*
	temperature	γ	0.63	0.20	3.16	*0.002*
	precipitation	γ	−0.15	0.15	−1.04	0.299
historical range (below 42°)	effort	p	0.11	0.03	3.54	*0.000*
$n = 539$ sites	date	p	−0.16	0.03	−5.63	*0.000*
	latitude	ψ	0.56	0.27	2.09	*0.037*
	proportion urban	γ	0.73	0.47	1.56	0.119
	elevation	γ	−0.63	0.34	−1.86	0.063
	housing density	γ	−0.34	0.42	−0.80	0.423
	temperature	γ	0.14	0.36	0.40	0.693
	precipitation	γ	0.12	0.31	0.38	0.704

support based on AIC ranking, indicating that covariates improved model fit. Following [11], to evaluate the adequacy of models we calculated the area under the curve (AUC) statistic [52,53] for each year for global models in the historical and expanded range. The AUC statistic represents the predictive power of each model for each year. Values of AUC lower than 0.70 indicate poor discriminatory power, 0.70–0.80 indicate acceptable discriminatory power and more than 0.80 indicate excellent discriminatory power [53].

To test the hypothesis that hummingbirds were more reliant upon nectar feeders in the expanded range compared with the historical range, we used a multi-season model and included all sites from 2002 to 2013 with nectar feeders and for which we had land cover data ($n = 905$ sites). We did not bin sites into the historical versus expanded range because we wanted to assess how detection varied across the entire latitudinal range. We included all site and observation covariates in the model and allowed detectability to vary with latitude. Detectability indicates the probability that a hummingbird will be detected at a site given that a hummingbird occupies the site. Therefore, modelling detection probability as a function of latitude at PFW sites can be interpreted as how likely it is for a hummingbird to visit nectar feeders at any given latitude (for a similar use of detection probability to infer feeder visitation rate, see [11]).

We used the presence and absence of hummingbird feeders reported by participants across years to document a pattern of northward expansion of supplementary nectar provisioning from 1997 to 2013 ($n = 2306$ sites). A feeder was considered 'present' at a site if the observer indicated that a hummingbird feeder was used at some point between November and April. We used mixed-effects logistic regression models, implemented with the R package lme4, to assess how the tendency to offer nectar feeders changed across years in the historical versus expanded range. In these models we treated year as a continuous predictor variable, feeder presence as a binary response variable, historical versus expanded range as a binary predictor variable and site ID as a random effect.

Finally, to visualize the northward expansion of hummingbirds in a manner quantitatively comparable with the northward expansion of nectar feeders, we calculated the proportion of sites from 1997 to 2013 ($n = 2306$ sites) supporting hummingbirds for each year in the historical and expanded range. Because these data included sites without nectar feeders and omitted details of repeated counts at sites, we did not use it for any quantitative comparisons, but present it for visual comparison only.

3. Results

The winter range expansion of the Anna's hummingbird northward along the west coast of North America from 1997 to 2013 was unambiguous (figures 1 and 2a, and table 1). Anna's hummingbirds were more likely to be found at colder sites in later years (figure 2b and table 1). Contrary to global temperature trends, mean minimum January temperatures at our sampling locations slightly decreased from 1997 to 2013 ($\beta = -0.117$ $t = -11.9$, $p < 0.001$ for 1269 sites in the historical range, and $\beta = -0.146$, $t = -14.4$, $p < 0.001$ for 1037 sites in the expanded range; figure 3a). Temperature was a significant predictor of colonization in the expanded range but not in the historical range, according to multi-season occupancy models (tables 2 and 3).

Housing density was a significant predictor of colonization in the expanded range but not in the historical range (tables 2 and 3). In the historical range, the only near-significant predictor of occupancy was elevation, with lower elevations tending to have higher occupancy probability (table 2). AIC model comparisons complemented these results (table 3); in the historical range, the highest-ranking model (ΔAIC < 2) included only elevation. In the expanded range, however, the highest-ranking model contained housing density and mean minimum January temperature. AUC statistics for

Table 3. Model selection for multi-season models for years 2002–2013 relating Anna's hummingbird colonization (γ) to site covariates in the historical range and the expanded range. Effort and date were included in all models as predictors of detection (p) and latitude as a predictor of occupancy (ψ).

location	model	parameters	AIC	ΔAIC	weight
expanded range (above 42°)	H + T	9	5091.6	0.00	0.57
$n = 366$ sites	H + T + P + U	11	5094.2	2.53	0.16
	H + T + E + P	11	5094.7	3.07	0.12
	H + T + E + U	11	5095.3	3.65	0.09
	H + T + E + P + U[a]	12	5096.2	4.53	0.06
	H + E + P + U	11	5103.7	12.1	0.00
	T + E + P + U	11	5109.0	17.3	0.00
	H	8	5112.0	20.4	0.00
	T	8	5122.9	31.3	0.00
	U	8	5128.7	37.1	0.00
	E	8	5132.2	40.6	0.00
	null	7	5151.0	59.4	0.00
	P	8	5152.1	60.4	0.00
historical range (below 42°)	E	8	8365.9	0.00	0.49
$n = 539$ sites	H + T + E + U	11	8368.5	2.61	0.13
	H + E + P + U	11	8368.5	2.62	0.13
	T + E + P + U	11	8369.0	3.11	0.10
	H + T + E + P + U[a]	12	8370.3	4.46	0.05
	H + T + E + P	11	8370.9	4.98	0.04
	H + T + P + U	11	8372.3	6.43	0.02
	T	8	8373.0	7.15	0.01
	H + T	9	8374.0	8.10	0.01
	U	8	8381.3	15.4	0.00
	H	8	8391.2	25.3	0.00
	null	7	8396.4	30.5	0.00
	P	8	8397.0	31.1	0.00

[a]Global model = housing density (H) + mean min January temperature (T) + elevation (E) + total January precipitation (P) + proportion urban land cover (U).

global models for each year indicated excellent discriminatory power in the expanded range (AUC mean ± s.d. = 0.82 ± 0.07 across years) and poor discriminatory power in the historical range (AUC mean ± s.d. = 0.64 ± 0.08 across years).

Hummingbird detectability (approx. 0.80 in global models) increased with increasing latitude despite decreased occupancy at higher latitudes ($\beta = 0.165$, s.e. = 0.024, $z = 6.86$, $p < 0.001$, $n = 905$ sites). Thus, sites that supported hummingbirds at higher latitudes were more likely to detect hummingbirds during count periods than sites at lower latitudes.

Finally, nectar provisioning by people increased over time in the expanded range, but not in the historical range. The proportion of participants with nectar feeders varied significantly among years at sites in the expanded range ($\beta = 0.351$, $z = 14.41$, $p < 0.001$, $n = 1037$ sites), but not in the historical range ($\beta = 0.038$, $z = 1.06$, $p = 0.287$, $n = 1269$ sites; figure 3b). People in the historical range were more likely to offer hummingbird feeders compared with people in the expanded range, with these proportions converging by 2009 ($\beta = -1.99$, $z = -2.00$, $p = 0.045$, $n = 2306$ sites; figure 3b). Likewise, the proportion of sites with hummingbirds in the historical and expanded range converged by the late 2000s (figure 3c).

4. Discussion

We documented a clear northward winter range expansion of Anna's hummingbird over the past 20 years using data from Project FeederWatch. We found strong support for the hypothesis that the range expansion was facilitated by urbanization and provisioning of supplementary food resources. First, we found that Anna's hummingbirds have been colonizing colder locations over time, suggesting that they are not merely following warming winter temperatures north. Despite long-term trends of increasing temperature in the Pacific Northwest [49,50], we found no evidence of a systematic and directional warming of winter temperatures at the sites in this study, suggesting that the time period was too brief to reflect these long-term changes or that the specific sites did not reflect this geographically broad trend.

Further, we found that Anna's hummingbirds were more associated with human-modified habitat in the expanded range than in the historical range. This suggests that urban habitat is most beneficial to these hummingbirds, where they experience the strongest thermal limits. The benefits provided by urban habitat could include the local retention of heat

(e.g. the 'heat island effect' [17]), increased availability of non-native flowers that bloom throughout the winter or increased availability of supplementary food (nectar feeders). Importantly, we found higher hummingbird detection probabilities with increasing latitude, despite lower hummingbird occupancy at higher latitudes. These higher detection probabilities at northern sites suggest higher visitation rates at feeders and potentially greater reliance on feeders at northern latitudes. This result complements recent work showing that some species may rely upon supplementary food to survive outside of their core environmental envelope (e.g. Eurasian blackcaps, *Sylvia atricapilla*, in England [31]; rose-ringed parakeets, *Psittacula krameri*, in Paris [33]). Similar analyses are warranted in ruby-throated hummingbirds (*Arhilochus colubris*), which are increasingly overwintering in the southeastern United States rather than migrating to Central America [34].

Finally, we found evidence that human behaviour may be changing along with hummingbird behaviour. There was an increased likelihood of people providing nectar feeders over time in the expanded range compared with the historical range. The hummingbird range expansion may have instigated a change in human behaviour, or increased provisioning of nectar feeders may have facilitated the hummingbird range expansion; it is likely that these two outcomes are intertwined. People in the expanded range who provide nectar feeders in summer may leave those feeders out later into the year if hummingbirds remain in the area, and those feeders may simultaneously enhance the winter survival of hummingbirds that do not migrate. Although we cannot disentangle these two patterns with our current dataset, we can conclude that more supplementary food resources are available to hummingbirds in the expanded range now compared with two decades ago.

The long-term ecological consequences of the Anna's hummingbird range expansion remain uncertain. Their expansion may affect the migratory or breeding behaviour of other hummingbirds. For example, rufous (*Selasphorus rufus*), calliope (*S. calliope*) and black-chinned (*A. alexandri*) hummingbirds breed in northwestern North America [35], and may experience increased competition with Anna's hummingbirds. Additionally, if humans are facilitating the range expansion to the extent that we suspect from this study, then it is unclear if the expansion would be sustained in the absence of supplementary nectar provisioning or non-native plantings. Assessing the indirect effects of range expansions on other species and the long-term dependence of native species on human-provided resources remains an important yet difficult task [20,21,25].

Understanding the nuances of how Anna's hummingbird migratory movements have changed over the past two decades will benefit from studies of marked individuals. Nonetheless, the broad pattern is clear: Anna's hummingbirds are more abundant in winter at northern latitudes now than they were several decades ago, implying a reduction in the proportion of individuals that migrate. Anna's hummingbirds are also more closely associated with human-modified landscapes in more northern latitudes, implying that people have facilitated this reduction in migratory behaviour and corresponding winter range expansion. Our study complements previous work showing that urban habitat and supplementary feeding may facilitate range expansions into colder climates [11,12,32,33] and potentially changes in migratory behaviour [13,14,31]. This pattern of human-assisted colonization is not unique to northward range shifts, as demonstrated by the colonization of novel areas by invasive species (e.g. Eurasian collared doves, *Streptopelia decaocto* [54,55]; house sparrows, *Passer domesticus* [56]), population growth around urban areas (e.g. Allen's hummingbird, *Selasphorus sasin* [57]), and even elevational range expansions (e.g. montane plants [58]). Overall, this work highlights how the effects of anthropogenic landscape modifications may interact with climate, in this case furthering northward expansion beyond what would be expected by historical thermal envelopes. It also highlights how our seemingly benign hobby of feeding birds may have far-reaching ecological consequences.

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