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RESEARCH ARTICLE

The establishment threat of the obligate brood-parasitic Pin-tailed Whydah (*Vidua macroura*) in North America and the Antilles

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ABSTRACT

The Pin-tailed Whydah (*Vidua macroura*) is a generalist obligate brood parasitic bird native to Africa, frequently found in the pet trade, which has successfully established exotic populations in 2 biodiversity hotspots in the Americas. We analyze the species' potential future distribution by identifying key locations in the continental United States, Hawaii, and the Antilles that contain suitable climatic characteristics, host species, and habitat requirements. We used species distribution modeling (MaxEnt) to depict the geographic patterns of possible Pin-tailed Whydah establishment and compared the predictive power of models that included combinations of climatic data ("climate"), land cover ("habitat"), and localities of historical and one known novel host ("hosts"). The preferred model, the "hosts" model, was the highest performing. The most important variable characterizing Pin-tailed Whydah distribution in the preferred model was the presence of a frequent historical host that is also established in the Americas, the Common Waxbill (*Estrilda astrild*), followed by a less frequent historical host, the Bronze Mannikin (*Spermestes cucullata*). Our research demonstrates that in the continental United States, Hawaii, and the Antilles, there are locations that possess the needed exotic host species that may facilitate further invasion by the Pin-tailed Whydah. Given that Pin-tailed Whydahs are known to exploit >20 host species from 4 families of birds, clear next steps include assessing their ability to parasitize novel, native species within the highly suitable areas identified in this research.

Keywords: brood parasite, invasive species, Pin-tailed Whydah, species distribution model, *Vidua macroura*

La amenaza del establecimiento del parásito de cría obligado *Vidua macroura* en Norteamérica y las Antillas

RESUMEN

Vidua macroura es un parásito de cría obligado y generalista nativo de África, encontrado frecuentemente en el comercio de mascotas, que ha establecido exitosamente poblaciones exóticas en dos puntos calientes de biodiversidad en las Américas. Analizamos la distribución potencial de esta especie en el futuro mediante la identificación de localidades clave en los Estados Unidos continentales, Hawai y las Antillas que presentan características climáticas, especies hospederas y requerimientos de hábitat adecuados. Usamos modelos de distribución de especies (MaxEnt) para delinear los patrones geográficos de un posible establecimiento de *V. macroura* y comparamos el poder predictivo de los modelos que incluyeron combinaciones de datos climáticos (*clima*), cobertura del paisaje (*hábitat*) y localidades de hospederos históricos y uno recientemente descubierto (*hospederos*). El modelo preferido, *hospederos*, fue el de mejor desempeño. La variable más importante para caracterizar la distribución de *V. macroura* en el mejor modelo fue la presencia de un hospedero histórico frecuente que también se ha establecido en las Américas, *Estrilda astrild*, seguido de un hospedero histórico menos frecuente, *Spermestes cucullata*. Nuestra investigación demuestra que en los Estados Unidos continentales, Hawai y las Antillas hay localidades con las especies exóticas necesarias que podrían facilitar una mayor invasión por parte de *V. macroura*. Dado que se sabe que esta especie tiene más de 20 especies hospederas en 4 familias, los pasos siguientes en la investigación incluyen determinar la habilidad de *V. macroura* para parasitar especies nuevas y nativas en las áreas de alta idoneidad identificadas en este trabajo.

Palabras clave: especies invasoras, modelos de distribución de especies, parásito de cría, *Vidua macroura*

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INTRODUCTION

Several obligate avian brood parasites have expanded their North American and Antillean range in recent decades and now pose a potential conservation threat to putative native host species in novel areas of their distribution (Pérez-Rivera 1986, Ortega 1998, Dinets et al. 2015). Foster parents raising brood-parasitic young typically experience losses in their own reproductive success, and some also have reduced annual survival (Rothstein 1990, Hauber 2003, Davies 2010). If these hosts coevolved with the brood parasite, they may have behavioral or life-history countermeasures that can reduce these costs of parasitism (De Mársico and Reboreda 2014). However, when the host is a novel species (i.e. has no coevolutionary history with the brood parasite), it typically experiences the full (if not increased) costs of parasitism. Some of the range-expanding brood parasites in the Americas involve icterid cowbirds (*Molothrus* spp.), which self-colonized new locations in the wake of, and likely as a result of, massive land-use transformations (Post and Wiley 1977, Pérez-Rivera 1986, Rothstein 1994, Ortega 1998). Here, we explore the potential for a new addition to this group, the Pin-tailed Whydah (*Vidua macroura*), a species heavily sold in pet markets (Raffaele 1989a, Moreno 1997) and one of the few obligate brood-parasitic finches in the genus *Vidua* that is also a host generalist (Lowther 2016) (Figure 1).

The Pin-tailed Whydah (hereafter "whydah") most commonly parasitizes the Common Waxbill (for scientific names of this and other host species, see Table 1) but also uses a variety of finch-like birds as hosts in its native range of central and southern Africa (Payne 2005, Lowther 2016). Of the 23 documented hosts in the native range (hereafter "historical hosts"), nearly half have been part of the pet trade, and 5 of them presently occur as established (locally breeding) exotic populations in North America and the Antilles (Table 1; Friedmann 1960, Payne 2005, Lowther 2016). These circumstances greatly increase the likelihood that the whydah can become an established exotic member of the avifauna in these regions. Whydahs have already established breeding and viable exotic populations in Puerto Rico (Raffaele 1989b) and, most likely, in southern California (Garrett and Garrett 2016). In Puerto Rico, whydahs were introduced during the 1960s and 1970s through accidental releases as part of the pet trade (Moreno 1997, Raffaele 1989a). On the island, they parasitize mostly exotic Orange-cheeked Waxbills, proving that the sequence of events necessary for successful invasion, from transportation to parasitizing hosts in a novel range, is possible. Additionally, whydahs have the ability to host-switch and parasitize novel species, even when the whydah has not evolved nestling mimicry toward these new hosts (Schuetz 2005a, Hauber and Kilner 2007, Lansverk et al. 2015). This trait increases the likelihood that whydahs will find, as suitable hosts, other non-African finches also established as exotics in North America and the Antilles. For example, in California, whydahs appear to parasitize the exotic Scaly-breasted Munia, an estrildid species native to Asia (Garrett and Garrett 2016).



FIGURE 1. Pin-tailed Whydah (*Vidua macroura*). Tibati, Cameroon. Photo credit: Eric Fishel

Species distribution models (SDMs) correlate species occurrence records with environmental attributes (e.g., climate, vegetation structure) to create a map depicting relative habitat suitability (Anderson et al. 2002, Rodríguez et al. 2007, Peterson et al. 2011). MaxEnt is a machine-learning SDM that has been used extensively to estimate habitat suitability for critically endangered species (Ibáñez et al. 2009), the potential geographic range of exotic species (Fernandez and Hamilton 2015), and the extent of suitable habitat in a future altered climate for whole taxonomic groups (Monterrubio-Rico et al. 2015). We used MaxEnt to create a map of relative habitat suitability for whydahs in the continental United States, Hawaii, and the Antilles. We consider such a map a necessary first stage in gauging the threat that whydahs pose to native birds in these locations. The maps are not sufficient, by themselves, to fully calculate invasion risk (see below). However, they do provide a way to quantitatively express where conditions are favorable for whydah occurrence and thus help prioritize monitoring and research efforts that can fully gauge risk (Stohlgren and Schnase 2006).

Initially, we used a standard approach to SDMs to identify locations where the basic climatic requirements of the whydah are met. This map is a baseline for where whydahs can reasonably be expected to occur in the future, based purely on abiotic requirements. We then extended the SDM to include a Land Use Land Cover (LULC) habitat covariate as a proxy for seeding grasses

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TABLE 1. Historical hosts and one known novel host of the Pin-tailed Whydah, with their frequency of parasitism, occurrence in the pet trade, and whether they have records in North America (Long 1981, Moulton and Pimm 1986, Lever 2005, Payne 2005, Schuetz 2005a, Pyle and Pyle 2009, Aagaard and Lockwood 2016, Birds Express 2016, Finch Farm 2016, Lowther 2016). Occurrence information was downloaded from the Global Biodiversity Information Facility (data accessed July 20, 2016). Species are ordered according to the Clements Checklist (Clements et al. 2016) and are separated by family (Chesser et al. 2016). Bold indicates species included in species distribution model(s).

Host	Frequent or rare host?	Traded?	Occurs in North America?
Ploceidae			
Scaly Weaver (*Sporopipes squamifrons*)	Rare	No	No
Village Weaver (*Ploceus cucullatus*)	Rare	No	No
Red-collared Widowbird (*Euplectes ardens*)	Rare	No	No
Long-tailed Widowbird (*E. progne*)	Rare	No	No
Grosbeak Weaver (*Amblyospiza albifrons*)	Rare	No	No
Estrildidae			
Swee Waxbill (*Coccopygia melanotis*)	Rare	Yes	No
Yellow-bellied Waxbill (*C. quartinia*)	Rare	Yes	No
Fawn-breasted Waxbill (*Estrilda paludicola*)	Rare	No	No
Orange-cheeked Waxbill (*E. melpoda*)	Rare	Yes	Yes [a]
Crimson-rumped Waxbill (*E. rhodopyga*)	Rare	No	No
Black-rumped Waxbill (*E. troglodytes*)	Rare	Yes	Yes [b]
Common Waxbill (*E. astrild*)	Frequent	Yes	Yes [c]
Black-crowned Waxbill (*E. nonnula*)	Rare	No	No
Black-cheeked Waxbill (*E. charmosyna*)	Rare	No	No
Red-billed Firefinch (*Lagonosticta senegala*)	Rare	Yes	No
Black-bellied Firefinch (*L. rara*)	Rare	No	No
African Firefinch (*L. rubricata*)	Rare	Yes	No
Zebra Waxbill (*Sporaeginthus subflavus*)	Rare	Yes	No
Bronze Mannikin (*Spermestes cucullata*)	Rare	Yes	Yes [d]
Magpie Mannikin (*S. fringilloides*)	Rare	Yes	No
African Silverbill (*Euodice cantans*)	Rare	Yes	Yes [e]
Scaly-breasted Munia (*Lonchura punctulata*)	Rare	Yes	Yes [f]
Fringillidae			
Streaky Seedeater (*Serinus striolatus*)	Rare	No	No
Emberizidae			
Golden-breasted Bunting (*Emberiza flaviventris*)	Rare	Yes	No

[a] Puerto Rico, southern California, Lesser Antilles, and Florida.
[b] Lesser Antilles.
[c] Hawaii and Lesser Antilles.
[d] Puerto Rico, southern California, and southern Texas.
[e] Hawaii.
[f] Puerto Rico, southern California, Georgia, Lesser Antilles, Florida, Hawaii, and southern Texas.

critical for the whydah's granivorous diet (Raffaele 1989b). We consider these abiotic and biotic suitability maps as conservative representations of where whydahs are likely to (at least) establish nascent populations. We then explored SDMs that explicitly recognize that, for the parasitic whydah, even highly suitable habitat will not be occupied if they cannot complete their life cycle by finding suitable host species (Friedmann 1960). We posit that the presence of any host individuals within suitable habitat is sufficient to create an initial bridgehead population of whydahs at that location. This bridgehead population provides the whydah the opportunity to expand to utilize other hosts (if needed) and subsequently grow its population and geographic range. For these SDMs, we assumed that whydahs will parasitize the 5 historical hosts and the 1 known novel host, the Scaly-breasted Munia, that occur in North America and the Antilles (Table 1).

METHODS

Species distribution models, in general, require known occurrence localities of a focal species and quantitative estimates of environmental conditions at those locations. Models are then fitted to environmental conditions at points where the species has been observed. These models can then be used to predict the habitat suitability of unsampled locations in geographic space, based on abiotic conditions in the model's environmental space (Peterson et al. 2011).

MaxEnt is a distribution modeling algorithm that requires geographic coordinates where the focal species

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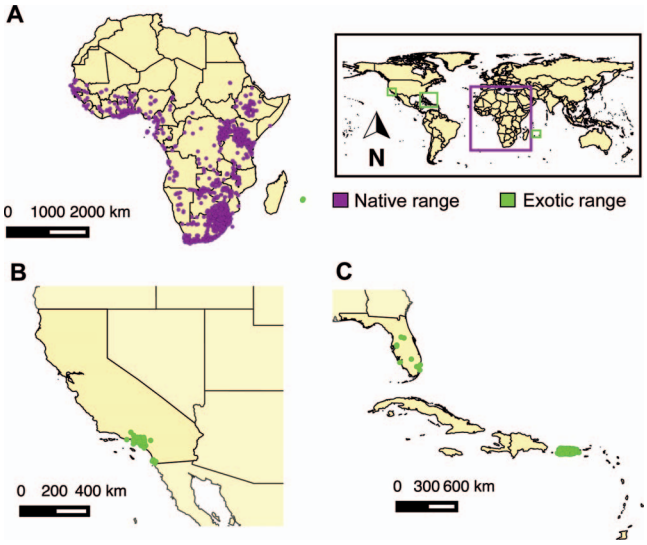


FIGURE 2. Georeferenced occurrence data for Pin-tailed Whydahs, used for generating species distribution models. All localities displayed here ($n = 2,329$) are human observations as reported to the Global Biodiversity Information Facility in both the native range (purple dots) and exotic range (green dots). We processed all occurrences by removing duplicates, spatially thinning, and excluding countries without established populations (that had no reports of breeding activity). We show the native distribution of the Pin-tailed Whydah in Africa (**A**) and exotic populations in California (**B**) and the Antilles and Florida (**C**).

is known to be present (Phillips et al. 2006, Merow et al. 2013). These points are then assigned a variety of attributes, which are provided by the model-builder and are thought by the latter to reflect environmental factors that dictate habitat suitability. From the attributes of these known-occurrence locations, MaxEnt builds a series of functions that quantitatively create a spatially interpolated map depicting where the species is likely to be found (Elith et al. 2011, Peterson et al. 2011, Merow et al. 2013). Suitability functions are evaluated by the model's ability to differentiate between the locations of known occurrence vs. a series of randomly selected other locations (i.e. pseudo-absences; Phillips et al. 2009). The key inputs to MaxEnt are the occurrence records for the focal species and the factors considered to be relevant attributes that define suitable locations. We describe this modeling approach below for our study species, the Pin-tailed Whydah, an invasive brood parasite.

Pin-tailed Whydah Occurrence Data

We sourced 39,279 georeferenced occurrences of whydahs worldwide from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/species). We removed duplicate records and those with missing longitude and/or latitude. Outliers were eliminated through 2 distinct steps: We confirmed that (1) all records were located within boundaries of the country indicated by the database and not associated with errors in coordinate transcription or museum specimens, and (2) data were filtered by retaining only those points that corresponded to countries with exotic breeding populations of whydahs identified through a literature search (Long 1981, Lever 2005, Garrett and Garrett 2016). Occurrence records were spatially thinned to a nearest-neighbor distance of 3 km using spThin (Aiello-Lammens et al. 2015). We selected a 3 km thinning distance based on the home range of the Shaft-tailed Whydah (*V. regia*), a congener of the Pin-tailed Whydah (Barnard 1990). In the absence of information on the dispersal range of the Pin-tailed Whydah, we used this information on its congener to estimate a distance beyond which observers are unlikely to record the same individual. Thinning the occurrence records also reduced the possibility that areas with a high density of occurrences due to biased sampling effort contributed a disproportionate amount to model training (see below). Our final input data on whydah occurrence included 2,329 points (Figure 2).

Attribute Variables

In an effort to characterize the abiotic conditions conducive to whydah occurrence, we included 19 WorldClim rasters that interpolate climate data for temperature and precipitation at a 5 arc-minute resolution worldwide (Hijmans et al. 2005). We used this set of climate variables to depict locations where abiotic conditions are conducive to whydah occurrence.

We recognize that whydahs, being granivorous finches, will be unable to survive in locations without seeding grasses to forage (Raffaele 1989b). Thus, we utilized the LULC database GlobCover to depict the location of vegetation that is likely to contain suitable forage (Arino et al. 2012). This LULC layer has 22 categories of land use, including 18 that quantify vegetation cover and 4 that indicate water (i.e. coastal habitat or river systems), artificial surfaces, ice, and barren areas. We used all 22 categories to identify vegetation and other land cover classes that may be important for predicting whydah distribution. We projected this layer to match WorldClim's 5 arc-minute resolution.

Finally, we included spatially explicit information on the localities of the 6 known historical or novel host species that occur as exotic populations in the continental United States, Hawaii, or the Antilles (Table 1). We had 2 options for doing so (Anderson 2017). The first was to generate SDMs for each host species and use these maps as input into the whydah SDM. The second was to use only the known point-occurrence records for host species as input into the whydah SDM. Both approaches were tested in situations similar to ours, where another species' presence

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TABLE 2. Model selection statistics for combinations of the covariates "climate," "hosts," and "habitat." We provide statistics for the models based on a split of occurrence records into training (75%) and testing (25%). Model fit in relation to the preferred model is shown by ΔAIC_c. *K* indicates the number of parameters used by MaxEnt to fit models. The preferred model has $AIC_c = 57{,}231$. Omission error rates assess the frequency at which preferred models incorrectly classified known Pin-tailed Whydah occurrences.

Model name	*K*	ΔAIC_c	Omission error rate
Hosts	26	0	0.26
Climate + hosts + habitat	148	516	0.13
Climate + hosts	146	604	0.13
Hosts + habitat	42	652	0.053
Climate	178	3,344	0.12
Climate + habitat	187	3,479	0.12
Habitat	16	17,560	0.12

is necessary for defining suitable habitat for the focal species (Hof et al. 2012, Giannini et al. 2013). In these prior studies, the latter approach (using only known point-occurrence records) consistently produced a better-performing model for the focal species (Giannini et al. 2013). For the whydah, its co-introduced hosts may be far from distributional equilibrium (Elith et al. 2010). Because the whydah is an obligate brood parasite, the species requires the presence of hosts; thus, realistic models should include only areas of known host occurrence.

Model Set and Selection

Using the above location attributes, we constructed 7 SDMs. The simplest were those that used only climate, habitat, or host information ("climate," "habitat," and "hosts" models, respectively; Table 2); we then created 4 additional models that represented all possible permutations of those 3 (Table 2). Once the model set was delineated, we evaluated the ability of each to predict whydah occurrence and used this information to select the single model that provided the most robust predictions (preferred model).

We selected the preferred model by using the sample-size-corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002, Warren and Seifert 2011). Model selection with AIC_c calculates the likelihood of estimated habitat suitability based on occurrence data. The AIC_c approach penalizes more complex models by accounting for the number of parameters used by each MaxEnt model (Swets 1988, Franklin 2009). We selected the preferred model that had the lowest AIC_c score. The preferred model's AIC_c score was subtracted from the AIC_c scores of all other models to indicate model relative fit (ΔAIC_c). We identified the most important covariates explaining variation in relative habitat suitability by determining the covariates that had the highest percent contribution.

For all 7 models, we applied a 10% minimum training presence threshold to MaxEnt's continuous output to produce a binary depiction of habitat suitability (Radosavljevic and Anderson 2014). Models were evaluated by testing their performance against 10,000 randomly sampled background points from 5-degree buffers around training occurrences (VanDerWal et al. 2009, Elith et al. 2011). Background points should be drawn from an extent potentially occupied by the focal species (Barve et al. 2011). The whydah is presently expanding its range, so we followed the work of Elith et al. (2010), who created SDMs for other invasive species and used a buffer to approximate a "reachable" extent within which we sampled background locations. Next, we created confusion matrices for each binary suitability map to assess their accuracy in terms of correctly identifying suitable vs. unsuitable habitat. We calculated omission rates to identify how often models labeled known suitable habitat as "unsuitable." To calculate omission rates, occurrence records were randomly partitioned into calibration (75%) and evaluation (25%) sets. We did not calculate commission rates because background points should not be used to evaluate model fit (Peterson et al. 2008).

Methods for incorporating biotic interactions as model covariates have been previously developed (Anderson 2017). These often involve consensus among several models (Giannini et al. 2013). If whydahs, as host generalists, can ultimately exploit a greater range of hosts than they currently do, a model based solely on known-host presence will underestimate their potential distribution and, thus, invasion risk. We may also underestimate whydah invasion risk if the parasite maintains the same suite of exotic hosts that it does now, but those hosts themselves expand their ranges. Several co-introduced historical hosts used by the whydah are indeed predicted to do so (Stiels et al. 2011, 2015). Recognizing the potential for changing biotic interactions, we created a congruence map that relaxes the assumption of host specificity and host range stability by combining suitability predictions for the strict "hosts" model and the more relaxed "climate" model. This approach follows previous work that has used 2 distribution models to portray variability in the importance of a biotic covariate (Pidgeon et al. 2015). We refrain from interpreting poorly performing models, but rather present the congruence map as a potentially more relevant risk map. We obtained a quantitative measure of the whydah's potential distribution by first converting suitability maps to the North America Albers Equal Area Conical projection. We then vectorized each map and used the QGIS (QGIS Development Team 2016) field calculator to determine areas indicating suitability (in meters squared, which we converted to kilometers squared).

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TABLE 3. Variable contribution of the 5 most important host covariates in the "hosts" model. A stochastic process determines the initial variable contribution, potentially masking variable importance if covariates are highly correlated; thus, we provide average values across 5 model iterations. For scientific names of species, see Table 1.

Variable	Contribution (%)
Common Waxbill	48
Bronze Mannikin	43
Scaly-breasted Munia	3
Orange-cheeked Waxbill	3
Black-rumped Waxbill	2

RESULTS

Our preferred model for predicting the potential distribution of the whydah is the "hosts" model (Table 2). This model had the lowest AIC_c across all permutations of model attributes. In this model, Common Waxbill and Bronze Mannikin had the highest percent contributions (48% and 43%, respectively; Table 3). The Scaly-breasted Munia, a known novel host of the whydah, ranked third in percent contribution (3%). Two less frequently used hosts, the Orange-cheeked Waxbill and Black-rumped Waxbill, ranked fourth and fifth in percent contribution (3% and 2%, respectively).

Our preferred model ("hosts") had a relatively high omission error rate (0.26; threshold = 0.035). Inspection of misclassified points indicated that these points were often near correctly classified locations. Moreover, the model misclassified only 2 points in the nonnative distribution, one in California and one in Florida. The remaining points in the nonnative range were correctly classified by our preferred model. The continuous habitat suitability map (Figure 3) demonstrates that the preferred model indicated high suitability in areas where there are one or multiple host species present: the West Coast of the United States, much of Hawaii, small sections of Texas and Florida, and many islands in the Antilles.

We created a congruence map (Figure 4) using the conservative "hosts" model and the liberal "climate" model to present a risk map showing where the whydah could potentially occur should it begin to exploit hosts other than the 6 we included here, or if the hosts themselves expand their geographic range. The "climate" model's highest contributing covariates were maximum temperature in the warmest month (31%) and precipitation in the driest month (17%). As expected, predictions in geographic space were more circumscribed for models built with only host information (27,184 km^2) when compared to the "climate" model (58,430 km^2). The congruence map further highlighted the high potential of the Hawaii archipelago and islands in the Antilles to be occupied by whydahs (Figure 4).

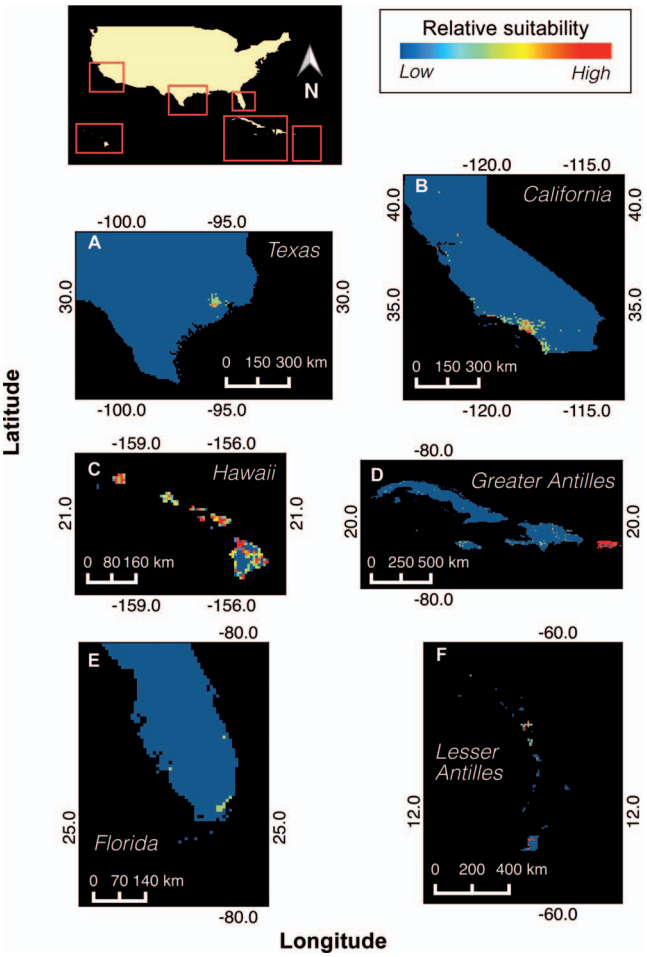


FIGURE 3. Geographic projection of relative suitability for Pin-tailed Whydah occurrence from the preferred MaxEnt model ("hosts") for (**A**) southern Texas, (**B**) southern California, (**C**) Hawaii, (**D**) the Greater Antilles, (**E**) southern Florida, and (**F**) the Lesser Antilles. Warmer colors indicate greater relative suitability for Pin-tailed Whydah occurrence, given presence of hosts.

DISCUSSION

Whether the whydah becomes the newest range-expanding brood parasite of conservation concern in North America, Hawaii, and the Antilles hinges primarily on the presence of suitable host species at the time of their initial establishment. Host information restricts our model to high suitability predicted in southern California, Hawaii, and several islands in the Caribbean. Contrary to previous work suggesting that climate and host information provides the best model fit for modeling parasite distribution (Giannini et al. 2013), our work suggests that for an obligate generalist brood-parasitic bird, host information alone provides the best fit.

Of the high-suitability areas we identify in the preferred model, only Puerto Rico and a small fraction of southern California are currently home to established whydah

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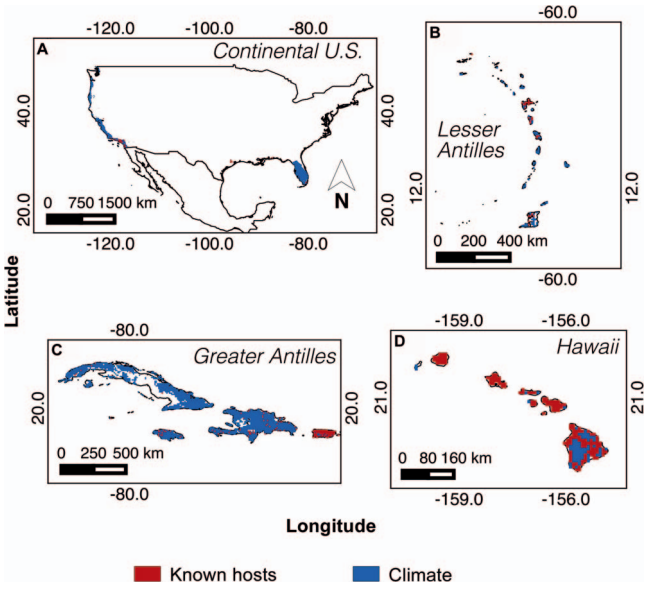


FIGURE 4. Congruence map showing agreement of two MaxEnt models of suitability for the Pin-tailed Whydah: "hosts" (our preferred model) and "climate." The more conservative geographic extent outlined in red (indicating areas identified as suitable by the "hosts" model) hinges on the assumption that the Pin-tailed Whydah will parasitize only the suite of historical hosts and one known novel host that we included in the "hosts" model, and that the hosts will not expand their range. The larger area outlined in blue (indicating areas identified as suitable by the "climate" model) is a more liberal projection that does not include host information. However, this more liberal predicted area may be relevant as a risk map if Pin-tailed Whydahs begin to use a greater range of hosts, or if the present suite of hosts expand their range in our focal area. Locations were classified as suitable by a 10% minimum training threshold. We highlight predictions for (**A**) the continental United States, (**B**) the Lesser Antilles, (**C**) the Greater Antilles, and (**D**) Hawaii.

populations. We suggest that Hawaii is poised to harbor a robust whydah population if released (again) in large enough numbers. Whydahs were regularly observed as free-living on Oahu during the 1960s through to the 1980s, indicating that they had the opportunity to escape captivity and become free-living in the past. These released individuals either failed to breed at all or the nascent population they established eventually became locally extinct, possibly due to co-occurring declines in populations of estrildid hosts on Oahu (Pyle and Pyle 2009). Nevertheless, our results show that all main islands in the Hawaii archipelago have large tracts showing suitable climatic conditions for the whydah, with historical host species now well established within several of these locations (Table 1).

If whydahs can switch to parasitizing other exotic finch hosts on Hawaii (e.g., Chestnut Munias [*Lonchura atricapilla*]; Pyle and Pyle 2009) or in Florida and the Antilles (e.g., Black-headed Munia [*Lonchura malacca*]; Lever 2005), their potential for establishment or range expansion may increase, provided that the climatic and habitat conditions of the region are suitable for occupancy (Duncan et al. 2001, Tatem and Hay 2007, Blackburn et al. 2009). By contrast, our preferred model may produce unrealistically high suitability estimates if biotic interactions (e.g., novel host species or food sources) are identified as important for whydahs at a smaller scale or extent than our attribute layers can portray (Wisz et al. 2013). Given a lack of consensus on methods for incorporating biotic covariates into SDMs (Anderson 2017), we believe that our congruence map best portrays the risk of whydah occurrence by depicting the difference between a highly circumscribed model taking account only of known host locations ("hosts") and a maximally liberal model constrained only by climatically suitable locations ("climate").

Given that recent whydah introductions are likely due to accidental releases of captive birds in the pet trade (Raffaele 1989b, Acevedo and Restrepo 2008), whether this species establishes within these locations depends on the number and spatial location of release events (Lockwood et al. 2005). Here, we utilize abiotic and biotic predictor variables to estimate potentially suitable habitat, but we have no way of depicting the probability of pet owners releasing whydahs and thus no suitable proxy for propagule pressure. As a step in this direction, future efforts to quantify establishment probability could estimate import or direct sales data for whydahs within our focal regions and use this as a proxy for propagule pressure (Blackburn et al. 2009).

Finally, in evaluating the risk of whydahs to native birds in our focal regions, we must address their ability and propensity to use native species as their hosts. Whydahs are remarkably flexible in the hosts they use in their native range (Payne 2005, Lowther 2016) and show the ability to successfully reproduce when expanding their host range (Lansverk et al. 2015). In order to reduce the possibility of a foster parent rejecting their young, whydahs mimic the mouth markings of the nestlings of their most frequent host species (Friedmann 1960, Payne 2005, Schuetz 2005b). This brood-parasitic adaptation initially would argue that whydahs are likely to be slow (or incapable) of switching to hosts with substantially different nestling gapes. However, mouth markings that are somewhat mismatched to hosts are clearly not prohibiting whydahs from experiencing reproductive success in the native (Payne 2005, Lansverk et al. 2015) and exotic range (Garrett and Garrett 2016). For example, Lansverk et al. (2015) provide evidence that whydahs experience similar reproductive success when parasitizing a novel host in Africa as they do with their more common hosts.

Despite the flexibility of host use in the whydah, we suggest that there are notable barriers for whydahs to surmount if they are to exploit as hosts the native avifaunas

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in our focal regions. It is not clear if the whydah is capable of making the jump from their usual small finch hosts to the suite of native species found in the West Coast of the United States, Florida, Hawaii, or the Antilles. So far, there have been no reports of whydahs parasitizing native species in Puerto Rico or southern California, although we found no evidence that anyone has been systematically looking for such events. We suggest that the most likely novel native hosts would be within the fringillid finches (Jetz et al. 2012). However, whydahs rarely exploit hosts with the open-cup nests typical of fringillids (Friedmann 1960); furthermore, hosts would need to accept the eggs and have a diet similar to that of whydahs (Davies 2010). In the Antilles, native finches (*Euphonia* spp.) build dome-shaped nests that may be more readily parasitized by whydahs, though their frugivorous (rather than granivorous) diet presents another barrier to parasitism (Raffaele 1989a).

The question of risk to native avifaunas is perhaps better posed as one of addressing how different gape markings, nest construction, and host diet must be before either (1) whydahs will not lay eggs in a host's nest or (2) whydah nestlings will be rejected by the host parents (*sensu* Schuetz 2005b). Posing this question in the context of the suite of possible native hosts within suitable whydah habitat we have identified here can substantially inform our understanding of the risk whydahs pose to the North American and Antillean avifaunas. The locations identified here as being suitable for whydah occupancy are native homes to a wide variety of bird species, many of which are threatened with extinction and are naive to brood parasitism. If whydahs were to successfully utilize them, the negative conservation and management impact on these new host species could be quite high.

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Author contributions: R.C.-O., J.L.L., P.C., and M.E.H. conceived the idea, design, and analyses and wrote the manuscript. R.C.-O. and J.L.L. analyzed the data.

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