

ECOLOGY, ECOSYSTEM SERVICES, AND CONSERVATION
OF ENDANGERED SCAVENGERS

by

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ABSTRACT

This dissertation reviews the global status of all avian scavenging birds, including vultures, and synthesizes in-depth fieldwork on the endangered Egyptian vulture *Neophron percnopterus* in the Middle East and Horn of Africa. Chapter 1 provides a succinct review of the ecology, status, and importance of vultures globally. Chapter 2 evaluates what ecological factors contribute to extinction risk for all 106 avian scavenger species globally. Combined, these chapters show that vultures, which are the only obligate vertebrate scavengers, have experienced the most rapid decline in conservation status of any group of birds over the past decade and comprise the most threatened avian functional guild in the world. By quickly locating and consuming carrion, vultures outcompete and control problematic facultative scavengers (like feral dogs and rats), insects, and microorganisms. When vulture populations decline, carrion becomes increasingly available to other organisms, in a form of terrestrial eutrophication. Furthermore, vultures' highly specialized digestive systems efficiently eradicate diseases when consuming carrion, whereas facultative scavengers are more susceptible to contracting and transmitting diseases among themselves and to humans. Diet, geography, body mass, clutch size, and taxonomy are all strong predictors of extinction risk, but dietary toxins are by far the most important anthropogenic threat to avian scavengers. Chapters 3 and 4 build on extensive fieldwork in the Middle East and the Horn of Africa and satellite-tracking of the endangered Egyptian vulture to illuminate habitat preferences, migration routes, and critical sites to target conservation actions. In Chapter

3, Egyptian vulture habitat use was investigated within home ranges and core use areas. Overall, vultures strongly selected for anthropogenic features, including highways and powerlines in arid areas. In Chapter 4, the most important migratory bottlenecks and stopover sites for the Egyptian vulture on the Red Sea Flyway were identified. Discouragingly, none of the area within the major migratory bottlenecks was protected and only <13% of the area within the major stopovers was protected. This demonstrates a very concerning gap in the protected area network. Combined, Chapters 3 and 4 provide clear guidelines where investment is urgently needed to help conserve endangered vultures in the Middle East and Horn of Africa.

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CHAPTER 1

VULTURES

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Quick guide

Vultures

Evan R. Buechley*
and Cagan H. Sekercioglu

What are vultures? Vultures are large, obligate scavenging birds that eat dead vertebrates. There are 23 species of vulture, inhabiting diverse biomes from the Amazonian rainforest and East African savannahs, to the Sahara Desert and high Himalayas. There are two main groups of vultures: Old World vultures of the Accipitridae family, found in Europe, Africa, and Asia, and New World vultures of the Cathartidae family, found in North and South America. It was long believed that New World vultures were more closely related to storks than to Old World vultures. However, recent molecular evidence indicates that they are likely to be sister taxa. Either way, the scavenging habits of these groups are thought to have evolved independently, leading to adaptations like large bodies, broad wings, powerful beaks and featherless heads.

How do vultures find and feast on rotting flesh? Carrion is a temporally and spatially unpredictable resource, which vultures are uniquely adapted to exploit. They soar to search for food over vast areas with minimal energy expenditure. Accordingly, vultures have some of the largest ranges of any animals on Earth. While only three of 23 vulture species are true long-distance migrants (turkey, black and Egyptian vultures), others, such as those in the genus *Gyps*, e.g. Eurasian griffon vultures, have individual foraging ranges of hundreds of thousands of square-kilometers (approximately the size of Spain). Vultures are also among the largest birds in the world, which enables them to store sufficient energy while covering vast distances in search of their next meal. For example, the Andean condor weighs over 11 kg and has an impressive wingspan of up to 3.2 m. Even more impressively, the extinct vulture *Argentavis magnificens* had a wingspan of approximately 7 m and a mass of around 80 kg.

Efficient energy management is a key adaptation of vultures. For instance, vultures' featherless heads were long thought to be an adaptation to keep



Figure 1. Vultures.
Critically Endangered white-backed vultures (*Gyps africanus*) in Ethiopia.

clean while foraging on rotting flesh. But, new research suggests that when vultures change posture, they can expose or cover large swaths of skin with their neck feathers allowing them to manage thermal radiation. Another unusual heat management adaptation is urohydration — or the New World vultures' habit of defecating and urinating on their legs, which provides evaporative cooling.

To efficiently locate carrion, vultures use cues from their cohorts. From their vantage point, high in the sky, most vulture species rely on vision to find food. This poses a challenge because carcasses are not moving and may be obstructed from view. However, when one bird finds and circles a carcass, it alerts its comrades of a potential meal. Soon, more curious vultures investigate, forming a 'kettle', a group of vultures circling a carcass, which indicates an impending feast to scavengers far and wide. Furthermore, New World vultures in the genus *Cathartes* also have a keen sense of smell: turkey vultures can locate

carrion under dense rainforest canopies or buried beneath leaf litter and can lead their relatives, the black and king vultures, to hidden meals they otherwise would not find. Mammalian scavengers, such as jackals and hyenas, also follow vultures, making them a keystone species of the scavenger community. Once they drop to a carcass, a group of feeding vultures, known as a 'wake', can facilitate ripping through tough hide, fend off competitors, and warn of potential threats.

Interestingly, vultures have highly specialized feeding niches. In the African savannah, Ruppell's and white-backed vultures gorge on internal organs; lappet-faced vultures use their powerful beaks to dine on ligaments and hide; white-headed and hooded vultures circle the feeding frenzy picking up scraps; and then the massive bearded vulture, the world's only vertebrate osteophage (bone-eating specialist), swallows large chunks of the skeleton whole or carries and drops the bones at an ossuary to break them into

smaller pieces. After the vultures' wake, often little remains of the carcass.

How are vultures doing? Nine of 23 vulture species (39%) are classed as 'Critically Endangered', i.e. on the brink of extinction (Figure 1). An additional three species are Endangered, four are Near Threatened, and seven are Least Concern. Over the past three decades, vultures have declined catastrophically, especially in Asia and Africa, and are now the most threatened group of bird in the world. Persecution, decreasing food availability, habitat destruction, and collision with energy infrastructure all threaten vultures. However, poisoning is the most imminent and dire threat, as it is incredibly effective at killing vultures. For example, in 2013, a single contaminated elephant carcass in Namibia killed 600 vultures.

Throughout Africa, vulture populations are crashing. Over three generations, the bearded vulture declined by 70%, while seven other species declined by 80% or more. Accordingly, four African vulture species were classed as Critically Endangered in 2015. The deliberate poisoning of mammalian carnivores, such as jackals, hyenas, and lions, to avenge livestock loss, has led to widespread unintentional poisoning of vultures. And now, with the boom of illegal rhino and elephant hunting across the continent, poachers are intentionally poisoning vultures because their carcass circling cues can quickly lead authorities to the scene of the crime.

The current acute situation in Africa is a worrying *déjà vu* of the extreme declines in South Asia, where populations of three vulture species declined by >95% between 1992 and 2007 due to poisoning from the anti-inflammatory veterinary drug Diclofenac. This drug, widely used to treat pain and swelling in sacred cattle, causes kidney failure in vultures after ingestion. Because of the drug's lethality and vultures' social foraging, only <1% of livestock carcasses would have needed to contain the drug to account for these declines. Encouragingly, India, Pakistan and Iran have banned the use of the drug for veterinary purposes, but it remains on the market in many other countries, including throughout Europe.

Why should we care about vulture declines? By quickly locating and consuming carrion, vultures

outcompete and control problematic facultative scavengers (like feral dogs and rats), insects, and microorganisms. When vulture populations decline, carrion becomes increasingly available to other organisms, in a form of terrestrial eutrophication. Currently, many facultative scavenger populations are increasing worldwide, causing significant top-down ecosystem effects via predation, invasion and competition. Furthermore, carcasses provide a reservoir and vector for many diseases, including rabies, chronic wasting, anthrax, bubonic plague, mad cow, foot and mouth, etc. Vultures have extremely acidic stomachs (pH = 1.0) where most viruses and bacteria cannot survive. When vultures eat carcasses, they actively remove these pathogens from the environment, as well as preempt the colonization and reproduction of pestilent insects.

Vultures offer valuable ecosystem services and are a fascinating group of birds highly adapted for their unique lifestyle. They have often been portrayed as malevolent creatures preying on the sick and weary. But the reality could not be further from the truth: vultures are the "soap of the savannah", quickly and efficiently removing waste, controlling pests, and preventing disease outbreaks — all free of charge. And, as true apex carnivores — eating all animals in the food chain, including lions, tigers, and bears — they are excellent indicators of ecosystem health.

Where can I find out more?

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Quick guide

Microbiology of death

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When a mammal dies, what happens? Decomposition happens. When a mammal dies its immune system shuts down, internal temperatures change, and internal bacteria begin to grow in ways impossible while under the constraints of a living host. The internal environment then experiences another major event: rupture — a break in the skin that allows air, microbes, and insects to enter, and bodily fluids to exit. A carcass releases large amounts of nitrogen into the environment, mostly in the form of ammonia, as well as carbon, phosphorus, and other nutrients important for life. A dead body becomes a hotspot of nutrients, water, and ecological activity.

How do we study mammalian decomposition? What is an anthropological research facility?

You may have heard the term 'body farm' in the news or on popular forensic science shows like *Bones* or *CSI*. In the scientific community, these research centers are more appropriately called 'anthropological research facilities', and are important for studying the anthropological, ecological, and forensic science implications of mammalian decomposition. Because of the interest in human decomposition for anthropology and its practical importance in forensic science, these facilities use human donors for field experiments to test the effects of different variables on taphonomy — the processes of decomposition. Some facilities also use pigs, which are good biological proxies for humans and allow for more replicates and better control over factors such as age, weight, and sex.

What organisms are involved in decomposition? Decomposition is one of the most important ecosystem processes — if it were not efficiently



CHAPTER 2

THE AVIAN SCAVENGER CRISIS: LOOMING EXTINCTIONS, TROPHIC CASCADES, AND LOSS OF CRITICAL ECOSYSTEM FUNCTIONS

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Review

The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions



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ABSTRACT

Vultures, which are the only obligate vertebrate scavengers, have experienced the most rapid decline in conservation status of any group of birds over the past decade and comprise the most threatened avian functional guild in the world. Of the 22 vulture species, nine are critically endangered, three are endangered, four are near threatened, and six are least concern. Meanwhile, the vast majority of avian facultative scavenger species, such as corvids and gulls, have stable or increasing populations. We analyze the causes of this stark contrast in status and evaluate what ecological factors contribute to extinction risk for all 106 avian scavenger species. A random forest model shows that diet breadth, proportion scavenged diet, geographic realm, body mass, clutch size and taxonomy are leading predictors of extinction risk. Meanwhile, dietary toxins – most notably poisons and the veterinary drug diclofenac – are by far the most important anthropogenic threat to avian scavengers, comprising the leading cause of decline for 59% of threatened avian scavenger species and 88% of threatened vulture species. Currently, 73% of vulture species are extinction-prone (near threatened, vulnerable, endangered, critically endangered and extinct) and 77% have declining populations, while only 13% of avian facultative scavenger species are extinction-prone and 70% have stable or increasing populations. As vultures decline, populations of many facultative scavengers are growing, causing trophic cascades from increased predation, competition, and invasion. Furthermore, vultures' highly specialized digestive systems efficiently eradicate diseases when consuming carrion, whereas facultative scavengers are more susceptible to contract and transmit diseases among themselves and to humans. We urge immediate action, particularly by regulating lethal dietary toxins, to prevent the extinction of vultures and loss of respective ecosystem services.

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1. Introduction

Scavenging, or the consumption of carrion, is a common foraging strategy and a critical component of ecosystem ecology (DeVault et al., 2003). Carrion is a spatially and temporarily unpredictable food source, which birds are particularly well adapted to exploit. Flight – particularly soaring – allows birds to cover large areas with little energetic expenditure, providing them with a competitive advantage over mammals in locating carrion. Indeed, an energetics model demonstrated that obligate vertebrate scavengers *must* be large soaring fliers (Ruxton and Houston, 2004). The 22 species of vultures in the world (the Palm Nut Vulture *Gypohierax angolensis*, is not directly related to other vultures, is not an obligate scavenger, and is excluded from this list) are the only obligate vertebrate scavengers, meaning they are near completely reliant on scavenging for food (while some vulture species, such as White-headed *Trigonoceps occipitalis* and Lappet-faced *Torgos trecheliotus* vultures, are known to kill live prey on occasion, they are highly dependent on carrion and are widely regarded as “obligate” scavengers). Vultures consume a large percentage of carrion globally—upwards of 90% in some ecosystems (Houston, 1986).

Over the last few decades, vulture populations have declined at catastrophic rates, especially in Asia and Africa (Buechley and Şekercioğlu, 2016; Ogada et al., 2012a, 2012b, 2015) and are now the single most threatened avian functional guild (obligate scavengers) in the world (Şekercioğlu et al., 2004). Meanwhile, many avian facultative scavengers (i.e. species that scavenge opportunistically) – including species of storks, gulls, ravens and crows – are among the most abundant bird species in the world, and, in many cases, have increasing population trends (IUCN, 2015). This stark contrast in the status of obligate and facultative scavengers led us to evaluate the factors causing this variable extinction risk.

In the first section of this review, we identify all avian scavengers and discuss differences in population trends between facultative, obligate and non-scavengers, and between vulture families (*Cathartidae* and *Accipitridae*). We then analyze differences in ecological traits of all avian scavengers to determine ecological predictors of extinction risk and review the extrinsic threats to avian scavengers. We conclude by reviewing the observed and expected ecological repercussions of vulture declines.

2. Material and methods

2.1. Scavenger classification and traits

A database containing ecological traits for all of the approximately 10,500+ bird species (hereafter “Birdbase”) was used to identify avian scavengers. Birdbase was compiled from an extensive literature survey of 248 sources initially (Şekercioğlu et al., 2004), is updated regularly with new publications (current version updated December 2015), and has been used in numerous global meta-analyses of bird populations (e.g. Şekercioğlu, 2012). Eight food categories are recognized – “invertebrates”, “fruits”, “nectar”, “seeds”, “land vertebrates”, “fish”, “scavenged matter”, and “non-reproductive plant material” – and ranked as a proportion of a species’ diet (see Kissling et al., 2011). This information was used to identify a comprehensive list of species for which scavenging accounts for >10% of their diet. We set the threshold at 10% because we wanted to capture a comprehensive list of species for which scavenging is a significant and regular feeding strategy, while

excluding the plethora of species that have been documented to scavenge rarely. This list of avian scavengers is a best estimate because it considers the foraging habits of every bird species in the world and is based on detailed species accounts from ornithological literature.

After identifying this group of avian scavengers, data were collected on the ecology, threat status, and population trend for each species. We also identified five families that account for 85% of all avian scavengers (*Accipitridae*, *Laridae*, *Corvidae*, *Falconidae*, and *Cathartidae*), and identified the threat status and population trend for each species within each family, including “non-scavengers” (species that receive <10% of their food from scavenging). The main sources for trait information, in addition to Birdbase, were the IUCN Red List of Threatened Species (2015); BirdLife International’s Data Zone (2015), and the Handbook of the Birds of the World (Hoyo et al. 1992–2014). When there was inadequate or conflicting information from these sources, the primary literature was consulted. In total, 11 traits were compiled (Table 1) and incorporated into a model to determine how ecological traits predict population trends. All independent variables included have been shown to be correlated with extinction risk (i.e. diet breadth, ecological specialization, body mass, generation length, maximum eggs per clutch, migratory status, habitat, island endemism, global range size) (Davidson et al., 2009; Gaston and Blackburn, 1995; Jones et al., 2006; Murray et al., 2011; Newmark et al., 2014; Purvis et al., 2000; Şekercioğlu, 2011; Sodhi et al., 2011) and/or were of particular interest in evaluating the population trends of avian scavengers (i.e. proportion scavenged diet, social foraging). To evaluate how phylogeny is related to population trends, we included family in the model (Davidson et al., 2012).

To evaluate extrinsic threats to avian scavengers, the leading threat for each extinction-prone species (including the IUCN categories of near threatened, vulnerable, endangered, critically endangered and extinct) was identified and grouped into one of six categories: persecution, habitat destruction, decreasing food availability, dietary toxins, fishery bycatch, or stochastic events.

2.2. Statistical analyses

Pearson’s chi-square test was used to identify whether differences in threat status (threatened, non-threatened) and population trend (increasing, decreasing) between groups of scavengers were significant. Standard residual values of ≥ 2 were used to conservatively identify the direction of the relationship at the $p < 0.05$ level (Agresti, 2012). A *t*-test for independent groups was used to evaluate differences in mean values of ecological traits (i.e. global range, max clutch, average mass, etc.) between scavenger groups. All statistical tests were conducted in R, version 3.0.2 (R Core Team, 2013).

To assess the relative trend in threat status between scavengers and all other foraging guilds over the past decade, we compared the percentage of extinction-prone (near threatened, vulnerable, endangered, critically endangered and extinct) species in each of eight major foraging guilds. To classify each species, we followed the methods of Şekercioğlu et al. (2004). These guilds are defined by primary diet and include species whose diet is >50% of each of the major food categories used in the Birdbase (described above). Species that do not receive a majority of their diet from a single food category are considered omnivores. Note that the definition for scavenger in this context is different from either obligate or facultative scavenger, as used throughout the rest of the analysis. This different definition was used to replicate the

Table 1
Description of traits used in the random forest (RF) analysis.

Trait	Description/source
<i>Population trend</i> (i.e. extinction risk)	From BirdLife's "Trend Justification" (BirdLife International, 2015). Categorized as: rapid decline (−3), moderate decline (−2), slight decline (−1), stable (0), slight increase (1), moderate increase (2), rapid increase (3). "Rapid" is indicative of >50% change in population over the past 3 generations, "moderate" of 25–50% change, and "slight" of <25% change. Species that were listed to be experiencing population increases or decreases without specific statistics were placed in the "slight" category. All species in this study had trend data, except for four (Española Mockingbird <i>Mimus macdonaldi</i> , Andean Gull <i>Larus serranus</i> , Slaty-backed Gull <i>Larus schistisagus</i> , Ruppell's Glossy Starling <i>Lamprolaima purpuroptera</i>), which are assumed to have stable populations. The Extinct Guadalupe Caracara has no trend and was excluded from the random forest analysis.
<i>Proportion scavenged diet</i>	The proportion (from 0 to 1) of a species' diet from scavenging on carrion. This variable originated from Birdbase, and was augmented by the Handbook of the Birds of the World (Hoyo et al., 1992) and primary literature on species (Feare and Craig, 1998; Ferguson-Lees, 2001; Howell and Dunn, 2007; Madge and Burn, 2001; Olsen and Larsson, 2013, 2004).
<i>Diet breadth</i>	The number of major food categories (from insects, fruits, nectar, seeds, vertebrates, fish, scavenged matter, non-reproductive plant matter) each bird uses. Ranked from 1 (the most specialized foragers, using only 1 major food type) to 8 (the most generalist foragers, using all 8 major food types) (Birdbase).
<i>Body mass</i>	Body mass, in grams (Birdbase).
<i>Generation length</i>	The average age of breeding adults in the population (BirdLife International, 2015).
<i>Max clutch</i>	The maximum number of eggs laid in a clutch (Birdbase).
<i>Migratory status</i>	Non-migrant, partial migrant, or full migrant (Birdbase).
<i>Habitat</i>	Either terrestrial or marine (Birdbase).
<i>Island restricted</i>	Island-restricted or not. Wide-ranging species of seabirds that breed on islands were defined as island-restricted because they are vulnerable to island-related threats. These species are Hall's Giant-petrel <i>Macronectes halli</i> , Antarctic Giant-petrel <i>Macronectes giganteus</i> , Great Shearwater <i>Puffinus gravis</i> , White-capped Albatross <i>Thalassarche steadi</i> and Campbell Albatross <i>Thalassarche impavida</i> .
<i>Global range</i>	Global range, in km ² (BirdLife International, 2015).
<i>Social foraging</i>	A rank of how socially a species forages: 1 = alone, 2 = in pairs, 3 = in small to medium sized groups, 4 = in a highly social manner with mixed species flocks (Birdbase).
<i>Realm</i>	Species were classified into 10 groups based on their geographic range: Australia (AU) (including New Zealand), East Asia (EA) (including India, the Indo–Malayan tropics, and southeast Asia), Afrotropical (AF) (continental Africa), Neotropical (NT) (southern Mexico through South America), Nearctic (NE) (central Mexico through North America), Palearctic (PA) (Europe and Asia minus EA above), Oceanic (OC) (oceans and oceanic islands), Old World (OW) (range extends over more than one of AU, EA, AF, PA), New World (NW) (range extends over NE and NT), or Cosmopolitan (CO) (range extends over NW and OW) (Birdbase).

classifications in Şekerciöğlü et al. (2004), in order to directly compare the percentage of extinction-prone species in 2004 and 2015.

To determine the relative importance of ecological traits in predicting population trends, we used random forest (RF) analyses. RF is a powerful machine-learning technique which identifies nonlinear associations among multiple correlated predictor variables (Cutler et al., 2007), as is the case in this study. RF analyses are growing in popularity in ecological studies, particularly those evaluating extinction risk, because they have several advantages over traditional linear models, including: 1) they do not assume data independence and therefore do not require a phylogenetic control; 2) categorical and continuous variables can be simultaneously incorporated into the model without transforming data; 3) they predict outcomes based on the nested structure of variables, which allows for an accurate depiction of different pathways to the predicted outcome; and 4) they are minimally affected by outliers (Davidson et al., 2009; Jones et al., 2006; Murray et al., 2011; Newmark et al., 2014; Sullivan et al., 2006).

The accuracy of the dependent variable can be a limiting factor in this type of analysis. Accordingly, extensive efforts were made to select and verify the quality of our dependent variable. While IUCN threat status has been used in some studies evaluating extinction risk (e.g. Cardillo et al., 2005; Davidson et al., 2009; Purvis et al., 2000), we use a more simply defined population trend variable. This variable is well suited for this analysis because it avoids potential issues from non-independence of dependent and predictor variables introduced when IUCN threat status is used (i.e. range size is incorporated in IUCN threat status determination). Many of the species in this study, including vultures, raptors, corvids, albatrosses and gulls are among the most studied of bird species in the world and, accordingly, population trends were available for >96% of species in this dataset (see below). Population trends originated from BirdLife International's Data Zone (2015), which summarizes the existing literature on each species, cites specific quantitative estimates of population trends, and weighs conflicting trend reports to decide on a final categorical trend estimate (i.e. increasing, stable, decreasing). Using the specific trend statistics included in the "Trend Justification" (BirdLife International, 2015), we re-categorized our trend variable into 7 categories: rapid decline, moderate decline, slight decline, stable, slight increase, moderate increase, rapid increase (see Table 1). In this context "rapid" is indicative of >50% change in

population over the past 3 generations, "moderate" of 25–50% change, and "slight" of <25% change. Species that were listed as "increasing" or "decreasing" without specific statistics were placed in the "slight" category. All species had trend data, except for four (Española Mockingbird *Mimus macdonaldi*, Andean Gull *Larus serranus*, Slaty-backed Gull *Larus schistisagus*, and Ruppell's Glossy Starling *Lamprolaima purpuroptera*), which are assumed to have stable populations. The extinct Guadalupe Caracara *Caracara lutosa* has no trend and was excluded from the RF analysis. While extensive efforts have been made to accurately assess and categorize the population trend data for all 106 species in this analysis, some population trend determinations are based on limited research and/or expert opinions. Note that conservation actions, such as extensive efforts to restore populations of the critically endangered California Condor *Gymnogyps californianus*, influence population trends and are therefore captured in the model.

The RF analysis was run in the *randomForest* package (Liaw and Wiener, 2002) in R (R Core Team, 2013). The number of trees (*ntree*) was set to 5000 (Newmark et al., 2014), and the optimal number of classification variables randomly sampled to calculate the split at each node (*mtry*) was determined by the program. A large number of trees are recommended, as RF does not over-fit data (Breiman and Cutler, 2015). The predictor variables were ranked in order of importance using the "mean decrease in accuracy" (MDA) output, which measures importance by calculating the average decrease in model accuracy when each variable is excluded (Liaw and Wiener, 2002). A higher MDA is indicative of a more important variable and variables that have no importance are close to zero, or even negative (Strobl et al., 2009). While some authors have used a z-test to determine the significance of predictor variables, Strobl et al. (2009) strongly urge against this: MDA values are statistically robust in and of themselves because they are based on many bootstrapped iterations of the data fitted to the set number of regression trees (5000 in this case).

3. Results

3.1. The avian scavenger community

Scavenging is an important foraging strategy (>10% of diet) for 106 bird species from five orders and 14 families. Of these, 22 species are

obligate scavengers (vultures) and 84 are facultative scavengers. Five families – *Accipitridae* (Old World vultures, eagles and hawks), *Laridae* (gulls), *Corvidae* (crows and ravens), *Falconidae* (caracaras and falcons), and *Cathartidae* (New World vultures) – account for 85% of all avian scavengers. Other species include sheathbills, petrels, shearwaters, albatrosses, storks, and starlings. Avian scavengers are truly cosmopolitan, inhabiting all continents, including Antarctica, as well as large portions of the world's oceans. Seventy-two species are terrestrial and 34 are marine. There are 10 island-restricted species, such as the Hood Mockingbird *M. macdonaldi*, which has a total range of only 70 km². Other species have immense ranges, like that of the Golden Eagle *Aquila chrysaetos*, which is found on four continents. Forty-six species are long-distance migrants, 57 are non-migrants, and 3 are partial migrants.

3.2. Threat status of avian scavengers

Of the 106 avian scavenger species, 25% (27) are extinction-prone (8 NT, 5 VU, 4 EN, 9 CR, and 1 EX), and the remaining 75% (79) are least concern (LC). Thirty-six percent (34) of species have stable populations, while 34% (41) are declining and 30% (30) are increasing (the extinct Guadalupe Caracara *C. lutosus* has no trend). Obligate scavengers have a significantly greater proportion of extinction-prone species than facultative scavengers ($\chi^2 = 34.261$, $df = 1$, $p < 0.001$), with 73% (16) of obligate scavenger species and only 13% (11) of facultative scavengers extinction-prone (Fig. 1). Obligate scavengers also have a significantly greater proportion of declining species ($\chi^2 = 6.992$, $df = 1$, $p = 0.008$) than facultative scavengers, with 77% (17) of obligate scavenger species declining and only 23% (5) stable or increasing and 29% (24) of facultative scavenger species declining and 70% (59) stable or increasing (Fig. 1). Average body mass is significantly greater for obligate (mean = 5629 g) than facultative scavengers (mean = 1282 g) ($t(104) = -8.79$, $p < 0.001$), generation length is significantly greater for obligate (mean = 15.74 years) than facultative (mean = 11.32 years) scavengers ($t(104) = -4.49$, $p < 0.001$), and clutch size is significantly greater for facultative (mean = 3.75 eggs) than obligate (mean = 1.50 eggs) scavengers ($t(104) = 6.96$, $p < 0.001$), illustrating that these groups have fundamentally different life histories. The *Accipitridae* family accounts for 67% (18 of 27) of extinction-prone species, followed by *Cathartidae*,

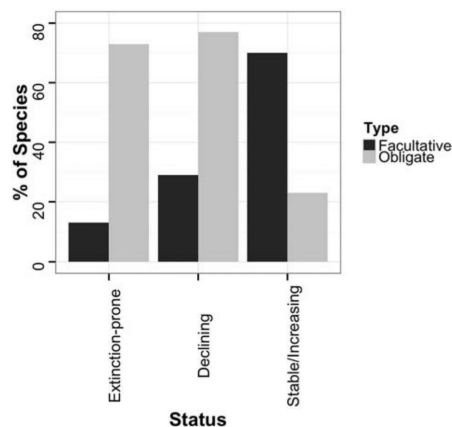


Fig. 1. The percent of obligate and facultative scavenger species that are extinction-prone and that have declining and stable or increasing populations. "Extinction-prone" species include those in the IUCN Red List category of Near Threatened, Vulnerable, Endangered, Critically Endangered, or Extinct (IUCN, 2015).

Diomedidae, and *Falconidae* with two species each, and *Ciconiidae*, *Laridae*, and *Mimidae* with one species each (Fig. 2).

Interestingly, within the five major families (*Accipitridae*, *Laridae*, *Corvidae*, *Falconidae*, and *Cathartidae*), facultative scavengers have a significantly smaller proportion of extinction-prone species than obligate scavengers ($\chi^2 = 30.349$, $df = 1$, $p = 0.001$) and non-scavengers ($\chi^2 = 8.518$, $df = 1$, $p = 0.003$) in their respective families. Furthermore, facultative scavengers have significantly more species with increasing population trends than obligate scavengers ($\chi^2 = 8.153$, $df = 2$, $p < 0.001$) and non-scavengers ($\chi^2 = 16.157$, $df = 2$, $p < 0.001$). This indicates that, in general, facultative scavengers are faring better than related species of obligate or non-scavengers.

3.3. Decadal change in avian guild threat statuses

Avian scavengers (in this context defined as species which receive >50% of their diet from scavenging, to directly compare with Şekercioğlu et al. (2004)) had by far the greatest increase of any foraging guild in the number of extinction-prone species over the past decade, increasing from 39% in 2004 to 56% in 2015 (Fig. 3). All other foraging guilds had an increase in the percent of extinction-prone species, except for granivores (seed eaters), which had a small decrease from 20% to 19%. Carnivores (vertebrate consumers, mainly raptors) had the second largest increase, from 22% extinction-prone in 2004 to 28% in 2015.

3.4. Ecological predictors of extinction risk

In decreasing order of importance, the major predictors of declining population trend (and hence higher extinction risk) in avian scavengers are taxonomy (family), diet breadth, proportion of diet that is scavenged, geographic realm, and body mass (Fig. 4). Habitat, generation length, social foraging behavior, being island-restricted, global range size, and migratory behavior had little to no predictive power, while clutch size had intermediate predictive power.

3.5. Extrinsic threats

Dietary toxins are the most prevalent extrinsic threat to avian scavengers, cited as the primary cause of decline in 59% (16 out of 27) of all threatened or near threatened avian scavenger species, and 88% (14 out of 16) of threatened or near threatened vulture species (Fig. 5). Other threats to avian scavengers include persecution (a leading driver of declines in 15% or 4 species), fishery bycatch (11%, 3 species), habitat loss (7%, 2 species), and decreasing food availability and stochastic events (4%, 1 species each) (Fig. 5). Fishery bycatch is a primary threat for marine scavengers, particularly albatrosses, as they are frequently caught in long-line ocean fishing operations. Stochastic events are a leading threat for the range-restricted island-endemic Española Mockingbird *M. macdonaldi*.

3.6. Comparisons among vulture families

Of the 22 vulture species, nine are critically endangered (CR), three are endangered (EN), four are near threatened (NT), and six are least concern (LC) (Fig. 6). A significantly greater proportion of Old World vulture (OWV) species are extinction-prone than are New World vultures (NWV) ($\chi^2 = 7.091$, $df = 1$, $p = 0.007$). NWV have significantly shorter generation lengths (mean = 13.73 years) than OWV (mean = 16.67 years) ($t(20) = 2.38$, $p = 0.027$), and smaller average mass (mean = 4438 g) than OWV (mean = 6185 g), although this is not significant ($t(20) = 1.17$, $p = 0.256$). It is worth noting that all NWV are least concern (LC), except for the California Condor *G. californianus* (critically endangered (CR)) and Andean Condor *Vultur gryphus* (near threatened (NT)). Condors are the two largest vulture species, by

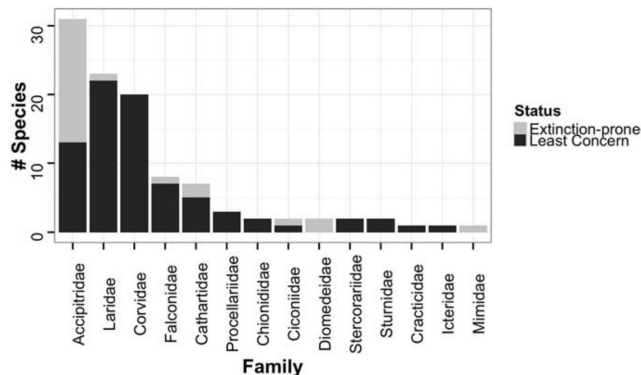


Fig. 2. The status of all avian scavenger species by family. “Extinction-prone” species include those in the IUCN Red List category of Near Threatened, Vulnerable, Endangered, Critically Endangered, or Extinct (IUCN, 2015). The Accipitridae family accounts for 67% of all (18 of 27) extinction-prone avian scavenger species.

mass, in the world, while four of the other five NWW are the smallest vultures in the world.

4. Discussion

4.1. Threat status of avian scavengers

Avian scavengers have disparate extinction risk and population trends. These differences are stark: specialist avian scavengers have experienced the largest increase in extinction-prone species (near threatened, vulnerable, endangered, critically endangered and extinct) of any guild over the past decade (Fig. 3), and obligate scavengers are the most threatened avian functional guild in the world, with 73% of species extinction-prone (Fig. 1). Meanwhile, only 13% of facultative scavengers are extinction-prone and over two-thirds (70%) of facultative scavengers have stable or increasing populations (Fig. 1). Within the 5 major scavenger families (Accipitridae, Laridae, Corvidae, Falconidae, and Cathartidae), facultative scavengers have significantly fewer extinction-prone and declining species than obligate scavengers or non-scavengers, indicating that facultative scavengers are particularly well adapted to exploit current environmental conditions. Such sharp declines of specialist scavengers and increases in generalist species are

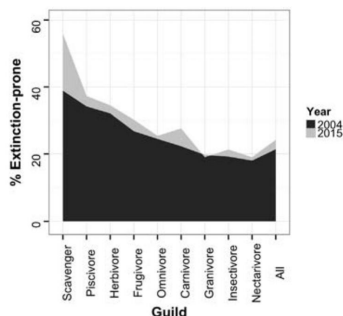


Fig. 3. The percent of species in each of 9 major feeding guilds that are extinction-prone (Near Threatened, Vulnerable, Endangered, Critically Endangered, or Extinct) in 2004 and in 2015 (IUCN, 2015). Note the particularly sharp increase in the threat status of avian scavengers.

indicative of a trend toward global functional homogenization (Clavel et al., 2011).

4.2. Ecological predictors of extinction risk

The primary predictors of extinction risk for avian scavengers are taxonomy (family), diet breadth, proportion scavenged diet, geographic realm, body mass, and clutch size (Fig. 4). These results support and augment existing models of extinction risk. It was expected that family would be the leading predictor of extinction risk, because Accipitridae vultures represent the majority of threatened species. Nonetheless other metrics had strong predictive power, indicating that there are broader ecological conclusions to be drawn from the model. Diet breadth and proportion scavenged diet, in particular, were leading predictors of extinction risk in avian scavengers. Diet specialization is a known predictor of extinction risk in a wide range of taxa, including plants (Rooney et al., 2007), fish (Munday, 2004), mammals (Fisher et al., 2003), and birds (Şekercioğlu, 2011, 2012), and population declines of birds have been shown to be strongly related to diet preference (Şekercioğlu et al., 2004). Geographic realm was another powerful

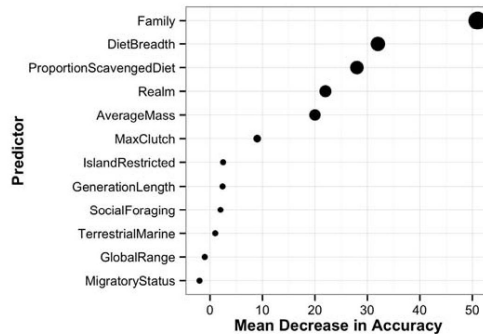


Fig. 4. Permutation importance scores for a random forest model evaluating the importance of ecological traits in predicting extinction risk in avian scavengers. Predictor variables are ranked in order of importance using the “Mean Decrease in Accuracy” (MDA) output, which measures the importance of each variable by calculating the average decrease in the model’s accuracy when that variable is excluded from the model. A higher MDA is indicative of a more important variable. See Table 1 for a full description of the variables.

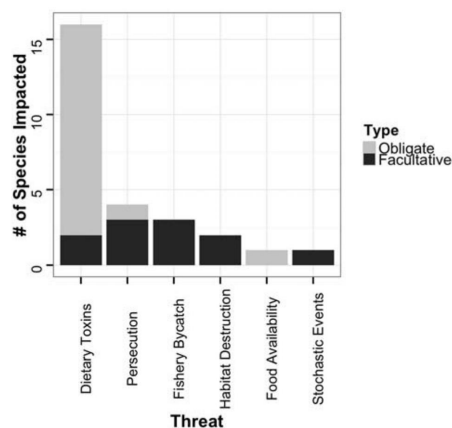


Fig. 5. Summary of the top extrinsic threats for each extinction-prone (Near Threatened, Vulnerable, Endangered, Critically Endangered, and Extinct) avian scavenger species. Threats are from species accounts in the IUCN Red List (IUCN, 2015).

predictor in our model, indicating that different species distributions, species-specific traits and, perhaps, anthropogenic practices on different continents play a role in scavenger declines. For example, the disparate use of poisons and veterinary drugs and differing human attitudes and degrees of governmental protection for wildlife are likely among the most important factors driving variations in extinction risk among avian scavengers, and the geographic realm variable may be capturing some of this influence. Body mass is another important predictor in our model, and has been shown to be an important factor in population declines in numerous studies across a wide range of taxa (Davidson et al., 2012; Dulvy and Reynolds, 2002; Gaston and Blackburn, 1995; Purvis et al., 2000). Large body size correlates with many other ecological traits that factor in extinction risk, including delayed maturation, slow reproductive rate, low population densities, and large individual home ranges (Purvis et al., 2000). Many avian scavengers, including vultures, eagles, albatrosses, and storks, are among the largest birds in the world. Finally, clutch size, like body mass, is another proxy for life history strategy, with smaller clutches indicative of *K*-selected species that are highly susceptible to increased adult mortality. Somewhat surprisingly, generation length (another proxy for overall life history), global

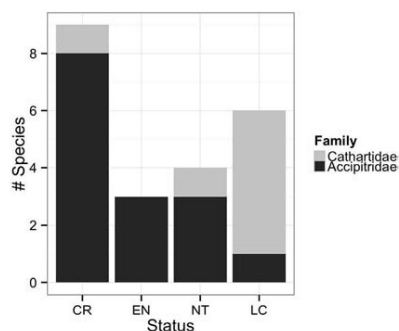


Fig. 6. IUCN threat status for all vulture species, by family (IUCN, 2015). *Accipitridae* vultures are significantly more extinction-prone than *Cathartidae* vultures.

range size, social foraging behavior, migratory status, being island-restricted, and habitat (broadly, terrestrial or marine) had no meaningful predictive power in the model. This is likely due to correlation with other variables in the analysis that are better predictors.

4.3. Extrinsic threats

The primary extrinsic threat for extinction-prone avian scavenger species is dietary toxins, followed distantly by persecution, fishery bycatch (a major factor in marine scavenger declines), habitat destruction, decreasing food availability, and stochastic events. Dietary toxins disproportionately threaten vultures, being the primary cause of decline for 86% (14 of 16) of threatened vulture species (Fig. 5). The most extreme example of dietary toxins causing declines comes from South Asia, where vulture populations declined by as much as 99.9% from 1992 to 2007 (Prakash et al., 2007). Poisoning from the anti-inflammatory veterinary drug diclofenac caused catastrophic declines of Oriental White-backed *Gyps bengalensis*, Long-billed *Gyps indicus*, Slender-billed *Gyps tenuirostris*, Egyptian *Neophron percnopterus*, and Red-headed *Sarcogyps calvus* vultures in India, Pakistan, and Nepal (Green et al., 2004). Vultures were exposed to diclofenac when they consumed carcasses of livestock that died within a few days of drug treatment (Oaks et al., 2004). Due to its extreme lethality to vultures, which manifests as kidney failure, and vultures' highly social foraging habits, only ~0.8% of livestock carcasses would have needed to contain diclofenac to cause such declines (Green et al., 2004).

Dietary toxins are causing vulture populations in Africa to crash, as well (Ogada et al., 2012a, 2012b, 2015). The deliberate poisoning of mammalian carnivores, such as jackals, hyenas and lions, to avenge the loss of livestock is common in Africa and has led to widespread unintentional poisoning of vultures (Ogada et al., 2012a, 2012b). With the recent escalation of rhino and elephant poaching across the continent, poachers are also now intentionally poisoning vultures, whose circling over carcasses can quickly lead authorities to the crime site (Ogada et al., 2015). *Carbofuran*, a widespread and cheap insecticide that is highly toxic is a primary culprit for such poisonings (Otieno et al., 2010; Virani et al., 2011). However, numerous types of poisons have been used throughout Africa, including *Strychnine* and synthetic organic pesticides. These poisons are incredibly effective at killing wildlife. For example, in 2013, a single poisoned elephant carcass in Namibia killed as many as 600 vultures (Buechley and Şekercioğlu, 2016; Smith, 2014). As a result of such poisoning, as well as other mortality factors, the Bearded Vulture *Gypaetus barbatus* has declined by 70%, while seven other species have declined by 80% or more over three generations across Africa (Ogada et al., 2015). Accordingly, the IUCN (2015) uplisted four vulture species (Hooded *Necrosyrtes monachus*, Ruppell's *Gyps rueppellii*, White-backed *Gyps africanus*, and White-headed *T. occipitalis*) to critically endangered (CR) in 2015, while another three species (Egyptian *N. percnopterus*, Lappet-faced *Torgos tracheliotus*, and Cape *Gyps coprotheres* vultures) are listed as endangered (EN), and the Bearded Vulture *G. barbatus* is considered near threatened (NT). In other regions of the world, including Europe and the Americas, dietary toxins, including rodenticides, insecticides (i.e. DDT), and lead from spent ammunition are contributing to mortalities of avian scavenger species. Thus, scavengers' vulnerability to toxins makes them indicators of environmental pollutants in the food chain, which impact countless other species across trophic levels.

4.4. Comparisons among vulture families

There are 22 species of vultures in the world in two distinct lineages: the New World vultures (NWV) in the *Cathartidae* family, and Old World vultures (OWV) in the *Accipitridae* family. NWV and OWV share many similar adaptations for scavenging, including large, broad wings adapted for long-distance, efficient soaring flight, and featherless heads, an adaptation for thermoregulation and/or to minimize

contamination while feeding on carcasses (Ward et al., 2008). Vultures in both families are K-selected species: they are long-lived, large-bodied and have slow reproductive rates. Interestingly however, NWV are significantly less threatened with extinction. Differing human practices and governmental policies for the protection of wildlife may factor in the disparate extinction risk of these similar groups of birds on different continents. Our results indicate that ecological traits may also play a role.

NWV have, on average, shorter mean generation lengths and smaller body masses than OWV, indicating a faster overall life-history strategy, which makes them somewhat less vulnerable to increased adult mortality. In support of this argument, the largest and slowest-reproducing NWV, the California *G. californianus* and Andean *V. gryphus* condors, are the only threatened NWV (critically endangered (CR) and near threatened (NT), respectively). We recognize that these factors are not necessarily the drivers of differences in these families, but find it noteworthy that important predictors of extinction risk in the overall dataset are significantly differentiated among these families. Perhaps a more important driver of the differences in threat status between vulture families, however, is differences in foraging ecology. In a key innovation that differentiates vulture families, NWV in the genus *Cathartes* have a highly developed sense of smell, which allows them to locate carcasses deep in forest, even when completely buried (Houston, 1985). They then lead other NWV species to carcasses that they would otherwise be unable to find. OWV, contrastingly, depend on vision to locate carcasses. NWV thus often eat smaller carcasses, including monkeys, sloths, birds and rodents, while OWV primarily eat larger carcasses, predominantly large ungulates. Trophic dynamics dictate that smaller animals are more numerous and ubiquitous in the environment, making them a more spatially and temporarily reliable food source. We also suspect that larger carcasses are more likely to contain environmental toxins, whether from veterinary drugs, intentionally applied poisons, or bioaccumulation. Furthermore, because of the social foraging habits of scavengers, a large carcass containing dietary toxins can be fed on by dozens (or even hundreds) of scavengers, whereas only a few individuals can feed on a small carcass. We suggest that this makes OWV at least somewhat more susceptible to poisoning than NWV—particularly those species in the *Cathartes* genus, which include no threatened species. While forest-dwelling NWV may be more susceptible to habitat loss (deforestation) than OWV, the main drivers of acute mortality—namely dietary toxins—are likely largely responsible for the apparently differentiated rates of decline between vulture families.

4.5. Repercussions of vulture declines

While research documenting vulture declines is extensive (Manga, 2006), there is little research investigating consequences of these declines (Markandya et al., 2008; Ogada et al., 2012a, 2012b). When vulture populations are reduced or removed from an ecosystem, carrion becomes increasingly available to other organisms, including facultative scavengers, insects, and microorganisms, in a form of terrestrial eutrophication. Furthermore, carcasses can serve as a breeding ground and vector for many diseases that impact wildlife, livestock, and humans.

There is strong competition among vertebrates, invertebrates, and microbes to use carrion (Putman, 1983). Nonetheless, vertebrate scavengers consume an estimated 75% of the available carrion globally (DeVault et al., 2003; Richardson, 1980). Vultures play a major role in locating and recycling carrion. In Central and South America, 60–95% of carcasses are located and consumed by vultures (Houston, 1985, 1994). In these studies, most carcasses were located within 12 h by Turkey Vultures *Cathartes aura*, whereas mammals rarely located carcasses. Due to their competitive advantage in finding and consuming carrion, Houston (1994) suggests that vultures likely consume more meat in Central and South America than all mammalian predators combined. Similarly, before their recent decline, vultures in the Serengeti of East Africa were estimated to consume about the same amount of meat

(370 kg/km²/year) as all mammalian carnivores in the ecosystem (Houston, 1983). Thus, rapid declines in vulture populations are expected to have profound and largely unanticipated impacts on ecosystem ecology.

First of all, mesopredator release is a major concern when apex predators are lost from an ecosystem (i.e. Soule et al., 1988), and we propose that this phenomenon can take place following vulture declines. There is growing evidence that trophic cascades follow the collapse of vulture populations. Due to facultative scavengers' faster reproductive rates (which we demonstrate here, i.e. shorter generation lengths and larger clutch size), they can reproduce more quickly when there are abundant resources. Over two-thirds (70%) of all avian facultative scavenger populations are currently stable or increasing, and they are faring better than obligate or non-scavengers within their respective families. Most facultative scavengers are also predators, and they can cause drastic top-down effects via predation, invasion, and competition when their numbers increase. Examples of subsidized avian facultative scavenger populations impacting lower trophic levels abound. For example, the California Gull *Larus californicus* population in the San Francisco Bay increased from <1000 breeding pairs in 1982 to >33,000 in 2006, as a result of increased availability of human refuse (Ackerman et al., 2006). This subsidized gull population was responsible for the depredation of 61% of American Avocet *Recurvirostra americana* chicks and 23% of Black-necked Stilt *Himantopus mexicanus* chicks at a shorebird colony (Ackerman et al., 2006). Nest predation increased in Ohio with the presence of facultative scavengers along a rural to urban gradient (Rodewald et al., 2011). In the Canary Islands, predation risk for ground nesting birds was higher near “vulture restaurants”, due to the subsidization of facultative scavenger populations at these sites, which, in turn, preyed on ground-nesting birds (Cortés-Avizanda et al., 2009). Large Kelp Gull *Larus dominicanus* populations in Argentina even increase whale mortality by feeding on the blubber of live whales when they surface to breathe (Marón et al., 2015).

Facultative scavengers are also often very successful invasive species: of the 56 animals on the 100 Worst Invasive Species list, 27 – or nearly half – are facultative scavengers (Lowe et al., 2000; Wilson and Wolkovich, 2011). In a particularly notorious example, the facultative scavenging habits of rats have, at least in part, enabled them to invade ecosystems. Ship Rats *Rattus rattus* are associated with global declines or extinctions of 60 vertebrate species (Towns et al., 2006). We expect the increased availability of carrion caused by vulture declines to exacerbate the magnitude and variety of such impacts, allowing some populations of facultative scavengers, mesopredators, and invasive species to increase in areas where vultures have declined, from human-dominated to remote, largely untrammelled ecosystems. Climate change may further exacerbate this trend, as generalist, highly adaptable facultative scavengers are expected to be at a competitive advantage, as species ranges shift and trophic dynamics are strained (Wormworth and Sekerciöğlü, 2011).

Vultures also provide an important ecosystem service by quickly consuming carcasses that would otherwise fester with disease (Markandya et al., 2008; Şekerciöğlü 2006, Şekerciöğlü et al., 2016). Carcasses provide a reservoir and vector for many disease agents, including Ebola, plague, anthrax, rabies, etc. (e.g. Monroe et al., 2015; Ramsden and Johnston, 1975). Vultures have highly acidic stomachs (with a pH as low as 1) which kill most viruses and bacteria that are ingested (Houston and Cooper, 1975). In Kenya, the absence of vultures at carcasses correlated with longer decomposition times, increased numbers of mammals at carcasses (primarily hyenas and jackals), and increased direct contact between mammals at carcasses (Ogada et al., 2012a, 2012b). Increased contact among facultative scavengers is expected to increase the potential for disease transmission between themselves and ultimately to humans. South Asia provides an alarming example of this. In India, vulture populations declined by approximately 99% between 1992 and 2003 (Markandya et al., 2008). During this same time period, feral dog numbers increased by 7 million, despite widespread

sterilization programs (Markandya et al., 2008). This increase in dogs resulted in 39 million dog bites from 1992 to 2003, causing an estimated 48,000 human rabies mortalities in India (Markandya et al., 2008).

When sufficient scavenger populations are absent, alternative methods to dispose of animal carcasses can be highly controversial, ineffective, and/or expensive. For example, in the outbreak of foot and mouth disease (FMD) in the United Kingdom in 2001, over 6.5 million animals were disposed of and/or slaughtered (Scudamore et al., 2002). Carcasses were initially buried on farms, but this was soon banned, due to concerns about infecting water supplies. Incineration of carcasses drew widespread public opposition due to concerns for the smell and health risks of smoke. Eventually, the UK government resorted to mass burials in engineered landfills. The Netherlands was also hard hit by the FMD outbreak and, to manage the issue, they slaughtered infected livestock and froze them en masse due to a lack of adequate disposal options (de Klerk, 2002). The vulture population crash in South Asia even led to a religious crisis among Parsis, a sect of Zoroastrians, which relied on vultures to consume the body of their deceased in “sky burials” for millennia. With skies devoid of vultures, Parsis have struggled to find a method to dispose of their dead that is harmonious with their religious beliefs. These examples foreshadow potential widespread problems resulting from functional extinctions of vultures.

5. Conclusions

In recent decades, growing concern for the plight of vultures has led to increasing research and conservation on this critical functional group (Manga, 2006), achieving important results. Examples include successful efforts to save the California Condor *G. californianus* from the brink of extinction and to restore populations across western North America (Walters et al., 2010), widespread reintroductions of the Bearded Vulture *G. barbatus* in Europe (Frey and Walter, 1989; Simon et al., 2007), and the rapid response of India, Pakistan, and Nepal to ban the use of diclofenac for veterinary purposes, which led to the stabilization of crashing vulture populations there (Cuthbert et al., 2011; Prakash et al., 2012). While this trend is encouraging, more research and conservation actions are urgently needed, particularly in Africa (to stem rapid declines), South Asia (to restore critically endangered populations) and South and Central America (to investigate the status and trends of little studied species, particularly the Andean Condor *V. gryphus*, and King Sarcophagus *papa*, Greater Yellow-headed *Cathartes melambrotus*, and Lesser Yellow-headed *Cathartes burrovianus* vultures). Furthermore, there is a pressing need for more research valuing the ecosystem services provided by vultures and investigating the potential ramifications for their declines (e.g. Markandya et al., 2008; Ogada et al., 2012b). In particular, we urge research: 1) quantifying how much carrion vultures consume, 2) investigating the role of vultures in eradicating and/or disseminating disease, and 3) determining how and to what degree vultures regulate populations of facultative scavengers and pestilent insects.

While further research is needed to better understand the consequences of vulture declines, it is clear that the widespread availability and application of dietary toxins is the most acute threat to their populations, as well as many other scavenging species. In order to prevent imminent extinctions of vultures and loss of invaluable and largely underappreciated ecosystem services, we urge regulations at local, regional, and global scales in order to inhibit the production, import, dissemination and/or misuse of lethal dietary toxins. While vultures have an intrinsic biological susceptibility to extinction in the modern world, the causes for their declines are definitively anthropogenic.

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CHAPTER 3

SATELLITE-TRACKING A WIDE-RANGING ENDANGERED VULTURE SPECIES TO TARGET CONSERVATION ACTIONS IN THE MIDDLE EAST AND HORN OF AFRICA

Evan R. Buechley, McGrady, M.J., and Şekercioğlu, C.H. (Forthcoming) Satellite Tracking a Wide-ranging Endangered Vulture Species to Target Conservation Actions in the Middle East and Horn of Africa. *Biodiversity and Conservation*.

Abstract

Vultures are the most endangered avian foraging guild (scavengers) and their loss from ecosystems can trigger trophic cascades, mesopredator release, and human rabies epidemics, indicating their keystone species status. However, vultures' extremely large home ranges, often crossing international borders, make conservation challenging. We provide a case study of how satellite-tracking data can be used to identify habitat preferences and critical sites to target conservation actions of wide-ranging species. We satellite tracked 16 endangered Egyptian vultures, *Neophron percnopterus*, in the Middle East and Horn of Africa. We used Brownian bridge movement models to calculate home ranges and core use areas (utilization distributions), and we analyzed habitat use in a resource selection framework. While median individual home ranges in both summer and winter were very large (5,106 km² and 2,333 km², respectively), summer and winter core use areas of all tracked Egyptian vultures were quite small by comparison (542 km², 185 km², respectively). This was caused by home ranges overlapping at critical sites where Egyptian vultures feed and roost and where conservation actions could focus. Our resource selection model successfully identified these core use areas and predicted the space use of Egyptian vultures throughout little studied regions. Overall, Egyptian vultures strongly selected for anthropogenic features, including highways and powerlines in arid areas. We used these results to identify protected areas and Important Bird Areas (IBAs), to rank them in order of importance, and to summarize the sites' conservation status.

Introduction

Vultures are the most endangered avian foraging guild (scavengers), with nine species Critically Endangered, three Endangered, four Near Threatened and six Least Concern (Buechley and Şekercioğlu 2016a; BirdLife International 2017). As vultures are lost from ecosystems, trophic cascades and mesopredator release (Buechley and Şekercioğlu 2016a; b) and human rabies epidemics (Markandya et al. 2008) can ensue, indicating their keystone species status (Mills, Soule and Doak 1993). Vultures' extremely large home ranges (e.g. García-Ripollés, López-López and Urios 2011), which often cross international borders and even continents (e.g. Opper et al. 2015), make conservation of these species particularly challenging. Nonetheless, advances in satellite tracking technology are enabling a revolution in our understanding of bird movements, migrations, and overall ecology (Bridge et al. 2011). Herein, we provide a case study of how vulture satellite-tracking data can be used to identify habitat preferences and critical sites to target conservation actions of wide-ranging endangered species.

Egyptian vulture, *Neophron percnopterus*, is an obligate scavenger that is largely a human commensal. It is distributed across southern Europe, central and southern Asia, the Middle East and Africa, with resident and long-distance migrant populations ((BirdLife International 2017). Migrants spend the Palearctic winter in areas that overlap largely with resident populations. In 2007, the Egyptian vulture was uplisted from Least Concern to Endangered due to widespread and sharp population declines, range contractions, and extinctions of populations, caused by inadvertent poisoning, electrocutions, collisions with wind turbines, reduced food availability, and persecution (BirdLife International 2017).

Egyptian vulture has been the focus of considerable research and conservation effort, mostly in Europe (e.g. López-López et al. 2014), and India (e.g. Cuthbert et al. 2006). Studies have illuminated Egyptian vulture movements and winter ecology of migrants (e.g. García-Ripollés et al. 2010), impacts of supplementary feeding (e.g. Monsarrat et al. 2013), ecosystem services (Gangoso et al. 2013), and population status and causes of declines (e.g. Cuthbert et al. 2006). Nonetheless, little is known about the status and ecology of the species across large swaths of its range, which hinders conservation planning. Sparse information from poorly known areas suggests that relatively large populations occur in some places, where threats are poorly understood. For example, Arkumarev et al. (2014) state that “the Afar region in Ethiopia is sheltering the most significant known wintering congregation of Egyptian vultures in eastern Africa... [approximately] 3% of the global population.” Meanwhile, the population in Turkey is estimated to be 1,500 to 3,000 pairs (Mendez, Donazar and Godoy 2015), likely larger than that of Spain (with an estimated 1,300 pairs (Cortés-Avizanda et al. 2009)). Recent surveys in Oman have identified some of the largest winter congregations ever recorded, with over 750 individuals counted at a single site in 2016 (J. Eriksen, personal communications).

We present results from the first multi-year (2013-2017) satellite tracking study of Egyptian vultures in the Middle East and the Horn of Africa—areas that are strongholds for the species but which have been minimally studied. We investigate differences in home range characteristics between age classes and breeding and nonbreeding individuals. We develop a resource selection model, and use it to generate predictive maps of Egyptian vulture space use. By overlaying them with maps of protected areas

and Important Bird Areas (IBAs), we highlight priority sites for conservation action. We then discuss the implications of our results for the conservation of this endangered species.

Methods

Vulture capture

During 2012-2015, we captured Egyptian vultures and fitted satellite transmitters to them in Turkey, Armenia, Ethiopia, and Djibouti. Permits were acquired for each country and year of capture. Egyptian vultures were captured near municipal waste dumps, where they reliably congregate (Al Fazari and McGrady 2016) using padded leg-hold traps with weakened springs to minimize the risk of injury (Bloom 1987). We trapped all individuals either after egg-laying or during the nonbreeding season, so as to minimize any potential influence on breeding (Lebeau et al. 2015). Captured individuals were measured, and checked for overall health. All were in good physical condition when tagged.

Egyptian vultures were fitted with solar-powered Global Positioning System Platform Transmitter Terminal (GPS PTT) transmitters (Microwave Telemetry, Ecotone Telemetry, North Star Telemetry, or DynaTrak), attached as backpacks with 8 mm Teflon ribbon (Bally Ribbon Mills, U.S.A). Transmitters weighed 24-45 g, <3% of body mass, as recommended (Klaassen and Hake 2014). Two transmitters from Microwave Telemetry, three from Ecotone, and one from DynaTrak used the Global System for Mobile Communications (GSM) network to transmit data. The other 10 units (five Microwave and five North Star) used the Argos Satellite Data Collection Relay System

Collect and Localization by Satellite (CLS America, USA). Two Microwave GSM units had maximum fix rates of one point per minute; all others had a maximum fix rate of one location per hour. Data were automatically downloaded and incorporated into the Movebank database (www.movebank.org).

Processing GPS telemetry data

Prior to analyses, all telemetry data were inspected and visualized in Movebank to check for outliers or potential dropped transmitters that continued to transmit. Using the Movebank facility, we removed erroneous fixes and only used the first location point for each individual in each hour to standardize the rate across transmitters, and reduce spatial and temporal autocorrelation (Walter et al. 2011). We also censored the first and last three days of data from each unit, so as to exclude data influenced by capture, transmitter failure, or death.

We segregated movement data on the summer range, winter range, and during migration, using piecewise regression to calculate migration start and end dates for those that migrated (Liminana et al. 2007). The data were subset by individual and calendar year, and a piecewise regression was fit to a plot of *latitude x time*. The point at which the regression splits delineated the summer, winter, and migrating stages. Migration data were excluded from analyses because migrating individuals may have been moving through large areas of otherwise unsuitable habitat, and so did not fit a resource selection framework. We identified whether adults were breeding in any given year by reviewing movement patterns during the breeding season, including regular, repeated visits to identified nest sites, and resightings of tagged adults in the field in Turkey and Armenia.

After processing our dataset, we had data on 16 individuals tracked over 28 summers and 23 winters.

Home ranges

We calculated 95% Brownian bridge movement model (BBMM) home ranges (Horne et al. 2007; Fischer, Walter and Avery 2013) for each animal, year, and season (summer or winter). Two individuals that were captured in Djibouti and Ethiopia did not migrate, so their home ranges were not split into separate seasons but calculated for the entire study period. The data for these individuals were included in the “winter” life-stage resource selection model, as their ranges overlapped extensively with those that were tagged in Turkey and Armenia that overwintered in the Horn of Africa ($n=12$).

Utilization distributions

We identified core use areas for both summer and winter seasons by developing a population-level utilization distribution (UD) (Palm et al. 2015; Watts et al. 2015). To do so, the probability distributions from each individual BBMM home range estimate was weighted by the number of location points and summed (Watts et al. 2015). Finally UDs were standardized to a value range from zero to one. We then produced a map of the final population-level UD for summer and winter to identify core use areas.

Environmental data

We created a geographic information system (GIS, using quantum geographic information system (QGIS: www.qgis.org)) with environmental data across the range of

point locations in the Middle East and the Horn of Africa. Due to the extremely large home ranges of Egyptian vultures—across several countries—and our desire to directly compare models of habitat selection between summer and winter, environmental data were limited to global data sources. Based on our knowledge of Egyptian vulture ecology and studies of space use (Oppel et al. 2015), we selected potential covariates likely to influence habitat selection. See the full list of covariates in Table 3.1.

After selecting these covariates, they were processed as follows. We reclassified the 23 global land cover types in our study areas to five categories to reduce model complexity and make the categories more ecologically relevant. Categories were “cropland” (composed of the GlobCover classes: 11, 14, 20, 30), “forest” (40, 50, 60, 70, 90, 100, 160, 170), “desert” (150, 200), “grassland” (120, 140), “savannah” (110, 130, 180), and “other” (190, 210, 220) (Oppel et al. 2015). We then produced raster layers for each category separately, by calculating the distance from each raster cell to each cover class (Burnham and Anderson 2002). We also included a tree density index (Crowther et al. 2015). Annual precipitation was calculated from monthly precipitation data. We included all paved road classes listed in OpenStreetMap (OSM) and merged them into a single highway layer. For powerlines, we included only the major transmission lines because Egyptian vultures are known to use large metal pylon transmission lines for perching and roosting, whereas small distribution lines are infrequently used (i.e. Arkumarev et al. 2014, Buechley personal observation). The “city” vector layer was defined by OSM as “the largest urban settlements in the territory,” normally with “a population of at least 100,000 people” and the “town” layer is defined as “a second tier urban settlement of local importance, often with a population of 10,000 people”

(OpenStreetMap 2016). We included both settlement types because our field observations suggest that Egyptian vultures avoid cities and congregate around towns to feed at garbage dumps. Using these line and point vector layers, we produced rasters by calculating the distance from each cell to each feature. Finally, we calculated a raster of terrain ruggedness from the digital elevation model (DEM), which can indicate nesting or roosting habitat. We then coarsened the resolution of both the DEM and ruggedness layers (from 90m), and resampled the livestock and human population density rasters (from 1km) to match the spatial resolution of the land cover data (300m). This 300m resolution was suitable for Egyptian vulture habitat use because the species is highly mobile and it was a good compromise between spatial resolution and computational size.

Model development, selection and predictions

We analyzed Egyptian vulture resource selection based on the second order selection procedure (Johnson 1980). We defined available habitat as occurring within the 95% minimum convex polygon (MCP) for all tracked individuals in each season. Distribution of habitats within the 95% MCP was determined by extracting covariate data systematically at 1km² density within this area (Benson 2013). Sampling environmental data at this density was satisfactory because it captured the diversity of covariate data at a small spatial resolution for a wide-ranging species. “Used” habitat was based on GPS locations from each tagged individual that fell within their 95% BBMM home ranges.

After extracting covariate data for each used and available point, we standardized all covariate data to aid with model convergence and allow comparisons between the relative influence of variables (Crandall, Bedrosian and Craighead 2015). We then

assessed the correlation of covariates by creating a correlation matrix using *corrplot* (Wei 2013), and assessed the variance inflation factors (VIF) using the *usdm* package (Naimi 2015) in R. We used a cutoff of $|r| = 0.60$ (Crandall, Bedrosian and Craighead 2015) as an indication of strong co-linearity, and had no co-linearity issues.

We used generalized linear models (GLMs) (Boyce et al. 2002) to model resource selection. We used an information theoretic approach (Burnham and Anderson 2002) for model selection by comparing the performance of models against one another following a manual backwards-stepwise model selection process (Domenech et al. 2015), as described in Hosmer and Lomeshow (2000). We modeled each covariate in isolation to determine if it had a significant effect ($p < .25$) on habitat selection. If it did not, it was excluded from any further modeling processes. We then built a global model with all covariates, and removed nonsignificant variables one by one in a backwards-stepwise manner until all remaining variables were significant ($p < 0.05$). We checked that the final model outperformed each candidate model, as well as the null model, using Aikake Information Criterion, adjusted for small sample sizes (AIC_c) (Bolker et al. 2009; Monsarrat et al. 2013) with the *AICcmodavg* package (Mazerolle and Mazerolle 2011) in R. We then calculated 95% confidence intervals for all coefficients in the final model to confirm their significance.

To test the predictive accuracy of our final models, we conducted k -fold internal cross validation with five folds following Boyce et al. 's (2002) methods. We stratified the k -fold selection to include roughly proportional numbers of both used and available points in each fold. To test if each of the five training models accurately predicted the final resource selection function (RSF) score of the points in the excluded fold, we

created a predictive map in the GIS based on each subset model, and binned the RSF values from the excluded points into 10 equal-area categories, based on their probability of occurrence. If the model performs well, there should be an increasing number of points from the excluded fold in the higher predictive bin categories. We tested for significance using the Spearman-rank correlation (Boyce et al. 2002; Crandall, Bedrosian and Craighead 2015). Lastly, we used the two final models (one for each season) to create a predictive map of the likelihood of Egyptian vulture occurrence over the 95% population-level MCPs.

Prioritizing conservation areas

To understand the importance of protected areas to Egyptian vultures and rank their relative importance, we overlapped both the population-level UDs and the predictive models (PM) of habitat use with protected areas (protectedplanet 2016) and Important Bird Areas (IBAs) (BirdLife International 2017), and summed use of each area using the zonal statistics plugin in QGIS, which summarizes the values of cells (Egyptian vulture use) within polygons (protected areas). This resulted in two values for each protected area: observed use and predicted use. We then calculated the relative importance of each protected area and IBA in relationship to the top site in each category. We list all of the protected areas that fall within the 95th percentile in each category (SI 1).

Results

We collected data from 16 individuals, tagged in Turkey ($n=10$), Armenia ($n=3$), Ethiopia ($n=2$), and Djibouti ($n=1$). Four of these were captured in their second calendar

year, three in their third year, one in its fourth year, one in its fifth year, and six were full adults. Two of the individuals tagged in the Horn of Africa did not migrate, but the third migrated and summered in Syria, Iraq, Iran, Turkey, Armenia, and Azerbaijan—in areas largely overlapping with those tagged in Turkey and Armenia. In total we analyzed 31,266 location fixes in the summer range (mean relocations/individual = 2,233 ($n=14$), range 105 – 12,281) and 49,939 location fixes in the winter range (mean relocations/individual = 3,567 ($n=14$), range 63 – 11,496) (Table 3.2).

Individuals caught as sub-adults (years 2-4, $n=9$) transmitted for a mean of 15.0 months (range 1 – 36); individuals caught and tagged as adults (5+ years, $n= 7$) transmitted for a mean 20.3 months (range 4 – 40). This is consistent with the expectation that adults would have higher annual survival, but is confounded by the different types of transmitters used. The DynaTrak transmitter ($n= 1$) transmitted for only 4 months, Ecotone transmitters ($n= 3$) transmitted for a mean of 7.7 months (range 3 – 16 months), NorthStar transmitters ($n= 5$) transmitted for a mean of 20.4 months (range 13 – 30), and Microwave transmitters ($n= 7$) transmitted for a mean 21.1 months (range 1 – 40) (Table 3.2).

Home ranges

Home ranges varied greatly by individual, season, and age class. The smallest recorded 95% BBMM home range was 218 km² for an adult in winter; the largest was 125,864 km² for a fourth year bird in summer. Home range size decreased with age; sub-adults had larger (and more variable) home ranges (mean = 26,570 km², SD = 36,739) than adults (mean = 2,853 km², SD = 3,401) ($t(10)=-2.13$, $p = 0.058$), and nonbreeding

adults (mean = 3,450 km², SD = 3,844) had larger home ranges than breeding adults (mean = 1,421 km², SD = 1,419) ($t(15) = -1.59$, $p = 0.133$). Summer home ranges were marginally larger (mean = 19,391 km², SD = 34,500) than winter home ranges (mean = 4,950 km², SD = 6,238) ($t(14) = 1.54$, $p = 0.146$).

Utilization distributions

While individual home ranges were generally very large, the core-use areas of the study population, as identified by the utilization distribution (UD), were roughly a magnitude smaller by comparison (Table 3.3). The 95% UD for the summer and winter were 542 and 184 km², respectively. This was caused by overlap in home ranges of multiple individuals at roosting and feeding sites (Figure 3.1).

Second order resource selection

Final models for both summer and winter seasons are summarized in Table 3.4. All model parameters in both season models were significant based on 95% confidence intervals that did not intersect zero. The average Spearman-rank correlation coefficient across RSF bins for the summer and winter models were 0.964 ($p < 0.001$) and 0.891 ($p = 0.001$), respectively, indicating that both models were highly effective at predicting Egyptian vulture resource selection. Furthermore, in the summer model, 95% of points withheld during k -fold cross validation fell within the top five RSF bins (ranked by probability of use), with 71% in the top bin; in the winter model, 97% were within the top five RSF bins, with 38% in the top bin (Figure 3.2). The ability of the models to accurately classify withheld points indicates strong support for their predictive power

(Boyce et al. 2002). The final predictive maps of space use within the 95% population-level MCPs are shown in Figure 3.3.

Prioritizing conservation areas

We identified protected areas and IBAs within the 95% population-level MCPs in both life-stages (summer and winter) and ranked them in order of observed and predicted importance. After identifying the relative importance of all protected areas and restricting the list to the top 95th percentile sites in each category (summer observed, summer predicted, winter observed, winter predicted), we identified a total of 27 important IBAs (16 summer, 11 winter) and 24 protected areas (12 summer, 12 winter). The median IBA has an area of 100,000 ha (range = 4,639-1,603,000 ha), while the median protected area is 180,650 ha (range = 2,200-4,536,600 ha). The status of most of the IBAs has not been recently assessed, and for those that have, 55% have a “very high” or “high” Threat Score, 86% have an “unfavorable” or “very unfavorable” Condition Score, and 100% have a “low” or “negligible” Action Score (Table 3.5) (BirdLife International 2017). Finally, only 19% of the IBAs we identified list the Egyptian vulture as a “trigger species”—species that are either threatened with extinction or that congregate in large numbers within an IBA. We found no information on the status of the protected areas identified.

Discussion

Egyptian vulture space use

While mean individual Egyptian vulture home ranges were vast, the 95% utilization distributions (UD) for our population in both summer and winter seasons were an order of magnitude smaller (Table 3.3). This is a striking result, indicating a very high level of concentrated overlap in space use by individuals of the population. This is important, indicating that conservation actions could focus on these relatively small areas where Egyptian vultures congregate to feed and roost.

In addition to documenting the specific locations of concentrated use for our study population from the UD, our resource selection models predicted Egyptian vulture habitat use throughout our study regions. Our second-order resource selection model successfully identified core use areas of our study population in both summer and winter ranges and successfully predicted points withheld during k -fold cross validation with a high level of accuracy.

In the summer model, anthropogenic factors played a large role in driving selection. Egyptian vultures strongly selected for proximity to highways and powerlines in arid areas. In particular, large metal power distribution pylons are heavily used by Egyptian vultures for both perching and roosting and our model indicates that their presence influences how individuals establish home ranges and core-use areas on a broad spatial scale. This is consistent with our observations of the species in eastern Turkey and Armenia. For example, we have noticed that Egyptian vultures are much more likely to feed at refuse dumps that have large pylons in the immediate vicinity. Egyptian vultures' strong selection for proximity to highways is not necessarily because

they are using them specifically (e.g. feeding on roadkill), but rather that highways serve as a proxy for human modification of the environment: where there are roads, there are likely to be people, garbage dumps, etc. Egyptian vultures also showed strong selection for proximity to towns in the model. In support of this, we often see the largest congregations of the species in the region at refuse dumps on the outskirts of towns. Egyptian vultures have long been known to be human commensals to varying degrees (e.g. Gangoso et al. 2013), and our summer model strongly indicates that they behave accordingly in this region. In terms of climactic and habitat variables, Egyptian vultures selected for arid areas, relatively low elevations, rugged areas, low tree density, and grassland, desert, and savannah habitats. It is interesting that individuals showed fairly strong avoidance of croplands, which make up a large proportion of the available habitat in the region, but this may be a correlate of selection for arid regions less suitable for crops.

The final winter model had some similarities and noteworthy differences from the summer model. While anthropogenic factors largely drove selection in summer, climatic factors primarily drove selection in winter. Individuals primarily selected for desert habitats at low elevations with low annual precipitation. They also selected for proximity to grasslands and, somewhat surprisingly, proximity to forests. This may be explained by their affinity for roosting in small patches of riparian forests in otherwise harsh deserts. Overall, they selected for areas with low tree density, which is consistent with Egyptian vultures reliance on vision to locate carrion. These habitat associations are somewhat different than those described for Egyptian vultures in Sahelian Africa in Opper et al. (2015), which found Egyptian vultures to favor savannah over deserts and crops over

grassland. However, our results are consistent with the Arkumarev et al. (2014) study of Egyptian vultures roosting location in relationship to habitat variables in northeastern Ethiopia. They found more roosting in harsher, desert environs with minimal vegetation cover, which is consistent with our model and observations in Ethiopia, Djibouti, and Somalia (Buechley, Şekercioğlu and McGrady, personal observations). As in the summer, individuals in our study selected for proximity to powerlines and towns, although these factors were much less important in the winter model. Egyptian vultures frequently perch and roost on large metal power transmission pylons in Ethiopia, Djibouti, and Somalia (Arkumarev et al. 2014; Buechley, Şekercioğlu and McGrady, personal observations), and feed extensively at garbage dumps on the outskirts of towns (Buechley, Şekercioğlu and McGrady, personal observations). However, our model indicates that these behaviors may be less of a driving factor for resource selection in the winter than the summer. Although, there are many villages and nomadic herdsman in the Horn of Africa—factors that we were unable to capture in the model. Based on detailed study of GPS locations overlaid on satellite imagery, we noticed that points often congregate around such small villages and cattle corrals, and we therefore believe that Egyptian vultures are highly human commensal in their winter range, as well. Unlike the summer model, they did not select for proximity to highways in the winter. This may be a somewhat spurious result, in that their primary winter range is in very harsh areas with little human development and few roads. Finally, they favored rugged areas in both seasons.

Prioritizing conservation areas

Identifying priority conservation areas is a top goal for the conservation of the Egyptian vulture in the Middle East and Africa (Dobrev et al. 2015), as it is for many endangered species. Using both population-level utilization distributions and final model predictions, we highlight protected areas and Important Bird Areas (IBAs) within both the summer and winter regions with both observed and predicted importance for Egyptian vultures. The list of sites that we identify should be considered a starting point for future research and conservation work in these regions, not a definitive list of the most important areas. For example, we recommend that future research in Iran could investigate Egyptian vulture occurrence at Kiamaki Wildlife Refuge (the protected area with the top predicted importance in the summer range), while conservation actions in Ethiopia could focus on the Afdem-Gewane Reserve (the protected area with the greatest observed use). In general, the most important protected areas and IBAs we documented for Egyptian vultures were located in Ethiopia, Turkey, Azerbaijan, Armenia, Iran, and Eritrea.

Protected area status

While protected areas carry at least some political designation of protection for landscapes and wildlife within their boundaries, the levels of funding, stewardship, and enforcement can vary greatly between protected areas (Leverington et al. 2010). Protected areas in developing countries often suffer from lack of funding and staffing and evaluation of protected area status and effectiveness are often lacking (Leverington et al. 2010), as is the case in this study. We were unable to find any reporting on the status of

the 24 protected areas we identified. Of the eight countries with key sites for Egyptian vulture conservation identified herein, four (Djibouti, Somalia, Turkey, Yemen) are among the least protected worldwide (Şekercioğlu et al. 2011a; Şekercioğlu et al. 2011b) with less than 5% of land cover falling within the World Database on Protected Areas (Juffe-Bignoli et al. 2014; Hsu 2016). Of the 27 IBAs we identified as important, 59% had no status or threat assessments at all. Of those that were assessed, the majority had high to very high threat scores (55%), unfavorable to very unfavorable conditions (86%), and low or negligible conservation actions taking place (100%) (Table 3.5). These results are similar to those by Horns et al. (2016), who identified and evaluated the status of IBAs throughout the Middle East and Africa that were used by migrant songbirds. Furthermore, only 19% of the IBAs we identified list the Egyptian vulture as a “trigger species”. Under Birdlife International’s Global IBA Criterion A1, a species should be listed as a trigger species for an IBA if... “[t]he site is known or thought regularly to hold significant numbers of a globally threatened species, or other species of global conservation concern” (BirdLife International 2017). Accordingly, we recommend that all 27 of the IBAs we identify here list the Egyptian vulture as a trigger species.

Conservation recommendations

While protected areas are an important tool in endangered species conservation, our resource selection models indicate that Egyptian vulture conservation must also take place outside of currently protected areas. Indeed, selection for anthropogenic factors, such as powerlines, highways, and towns, indicates that the species will not be protected by conservation actions in protected areas alone. To the contrary, the most important

immediate conservation actions should focus on widely documented acute threats, including dietary toxins (including poisons, lead from spent ammunition, and Nonsteroidal Anti-inflammatory Drugs), changing sanitary policies and management of dumps that are a major food source, electrocution on powerlines, and collision with wind turbines (e.g. Cuthbert et al. 2006, Angelov et al. 2012, Opper et al. 2016, Blanco et al. 2017).

Overall, our resource selection models and field observations in wintering and summering areas highlight Egyptian vultures' association with human settlements and infrastructure, in particular, their reliance on garbage dumps for food and their use of powerlines for perching and roosting. Dumps provide a major food source for many species, but are also likely a major source of dietary toxins (Garcia-Fernandez et al. 1995; Martínez-López et al. 2015). We recommend that waste management policies and activities be reviewed on a flyway scale with Egyptian vultures and other wildlife in mind. Additionally, Egyptian vultures' reliance on large pylons indicates that these structures are providing a resource to the species in the form of perching and roosting platforms. However, this benefit may come at a considerable risk. Powerline electrocution and collision is known as one of the primary causes of mortality in the species (e.g. Angelov et al. 2012). While the large metal transmission pylons that we regularly see Egyptian vultures perching on in both Turkey, Armenia, Ethiopia, and Djibouti (Figure 3.4) are expected to pose relatively little risk of electrocution because of the large distances between lines (Lehman, Kennedy and Savidge 2007), we recommend more research to identify whether such pylons are beneficial, or actually comprise an ecological trap. Going forward, dangerous powerlines should be modified, while newly

constructed powerlines should use existing bird-safe designs.

Conclusions

Conservation of wide-ranging endangered species poses significant challenges. However, combining research on known causes of mortality with resource selection models and utilization distributions derived from telemetry data can help prioritize specific sites for conservation actions. In this case study of the wide-ranging endangered Egyptian vulture, utilization distributions and predictive resource selection models show highly concentrated space use, indicating target areas where future conservation actions could be focused.

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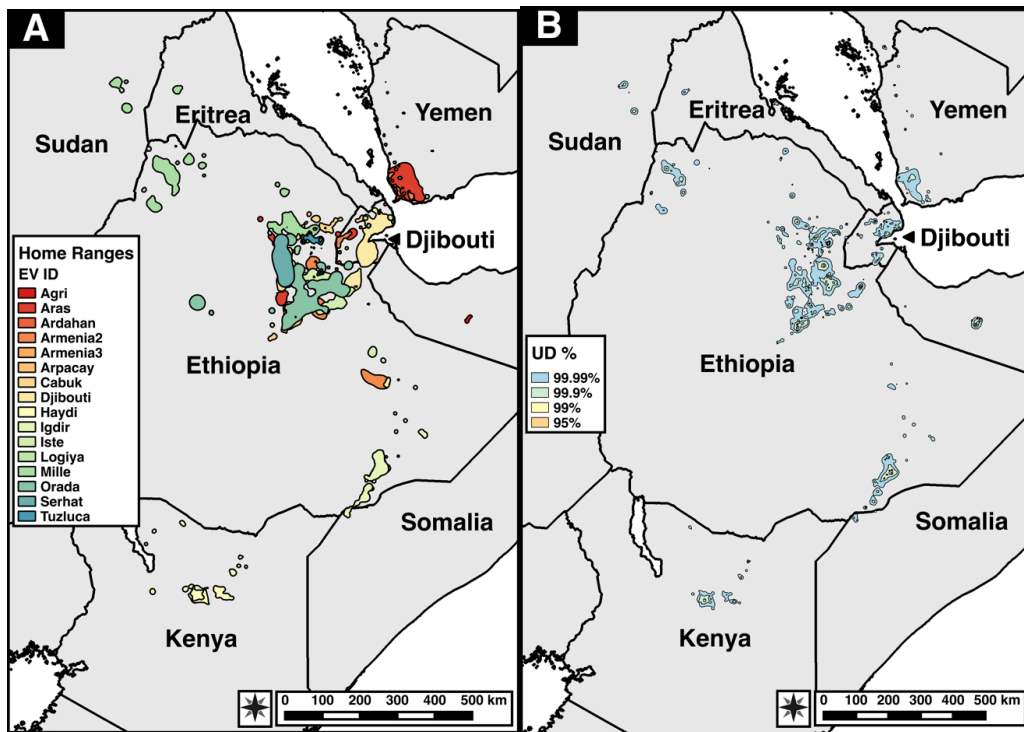


Figure 3.1. Maps of A) the individual-level 95% Brownian bridge movement model (BBMM) home ranges and B) population-level utilization distribution (UD) for the “winter” life stage. In addition to the 95% UD, we also included the 99%, 99.9% and 99.99% UD’s to aid in visualizing the core areas that were used by Egyptian vultures.

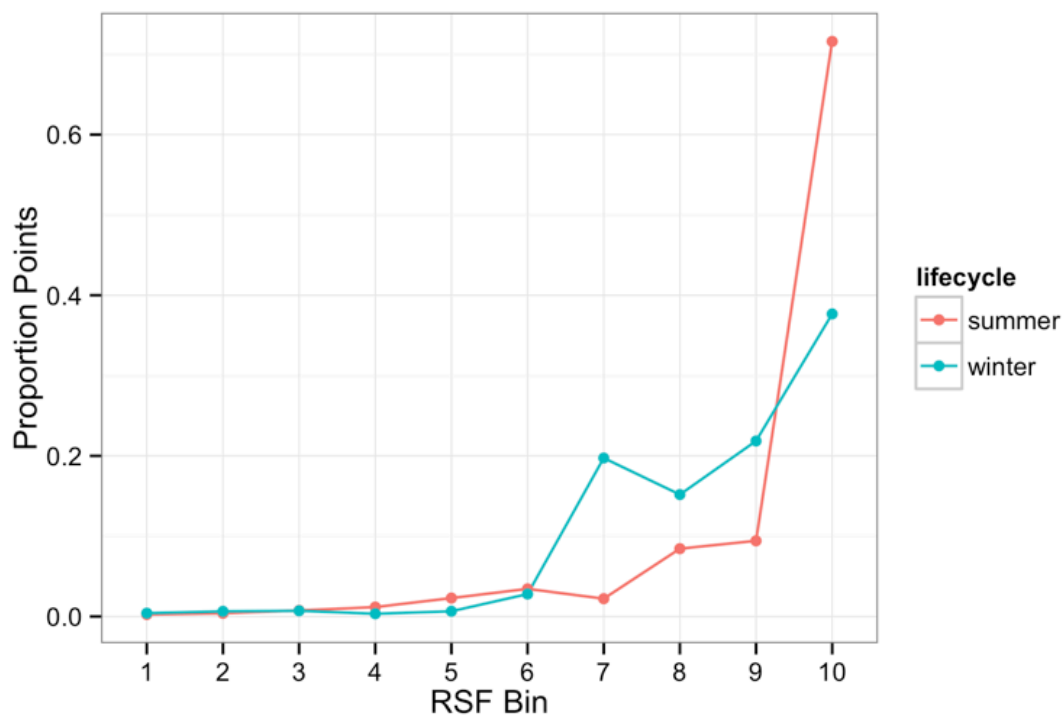


Figure 3.2. The averaged proportion of Egyptian vulture locations withheld during 5-fold cross validation that were classified into each RSF bin. A lower RSF bin (i.e. 1) indicates a low probability of use, and a higher bin (i.e. 10) indicates a high probability of use. Both summer and winter models predicted space use well, with more withheld locations falling in high bin categories.

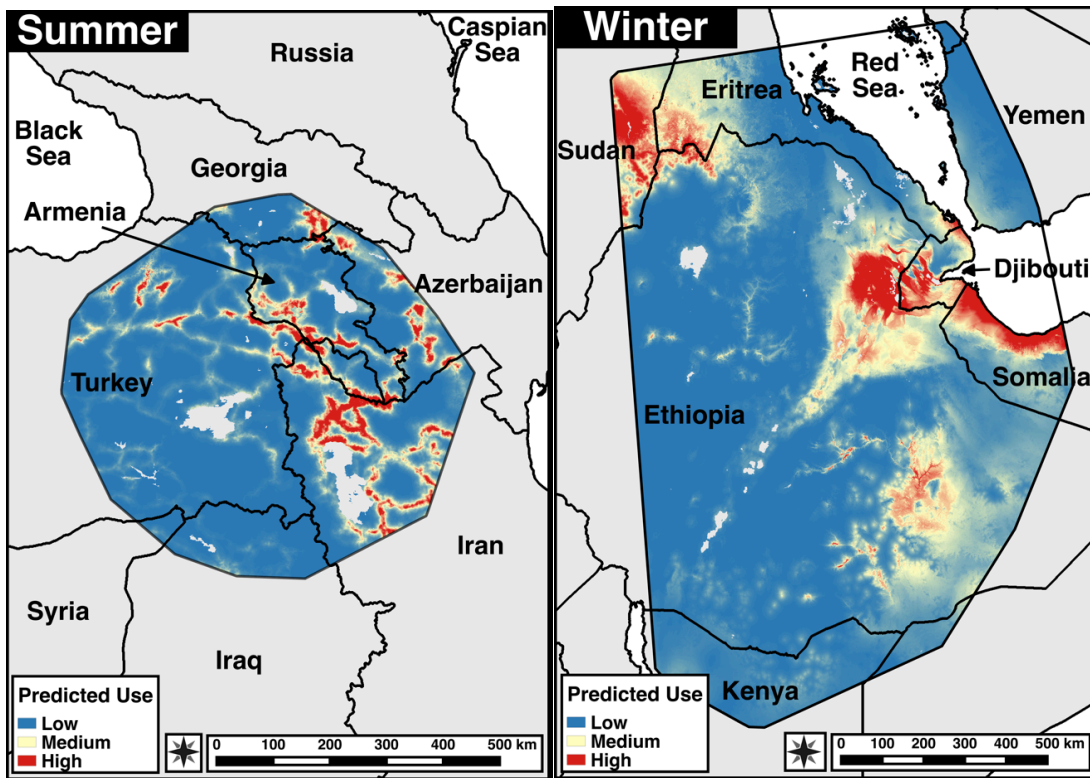


Figure 3.3. Predicted Egyptian vulture habitat use within A) summer and B) winter 95% population-level MCPs. Note that the summer model was strongly influenced by linear anthropogenic features (e.g. powerlines and highways).



Figure 3.4. Egyptian vultures strongly selected for proximity to powerlines in both summer and winter ranges. We observed large congregations roosting on large metal power transmission pylons in both regions, such as those pictured here.

Table 3.1. Environmental covariates included in the resource selection models.

Model Covariate	Source
global land cover class	GlobCover 2009; http://due.esrin.esa.int/page_globcover.php
tree density	Global tree density; http://elischolar.library.yale.edu/yale_fes_data/1/
elevation	NASA Shuttle Radar Topographic Mission (SRTM) 90m Digital Elevation Model (DEM), http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1
ruggedness	NASA Shuttle Radar Topographic Mission (SRTM) 90m Digital Elevation Model (DEM), http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1
cow density	Livestock Geo-Wiki, http://www.livestock.geo-wiki.org
goat density	Livestock Geo-Wiki, http://www.livestock.geo-wiki.org
sheep density	Livestock Geo-Wiki, http://www.livestock.geo-wiki.org
human population density	Gridded Population of the World (GPW) v3, http://sedac.ciesin.columbia.edu/data/collection/gpw-v3
distance to cities	OpenStreetMap (OSM), http://www.openstreetmap.org
distance to towns	OpenStreetMap (OSM), http://www.openstreetmap.org
distance to powerlines	OpenStreetMap (OSM), http://www.openstreetmap.org
distance to highways	OpenStreetMap (OSM), http://www.openstreetmap.org
precipitation	Global Climate Data, http://www.worldclim.org

Table 3.2. Summary of tracking dataset.

ID	Age at Capture	Capture Date	Months Data	Total Locations	Summer Locations	Winter Locations	Transmitter Manufacturer	Fate
Aras	2	Aug-12	7	1698	105	1593	Microwave	Missing, Ethiopia
Arpaçay	3	Aug-12	1	169	169	0	Microwave	Dead, Iraq
Iğdir	Ad	Aug-12	31	8820	2606	6214	Microwave	Dead, Ethiopia
Djibouti	4	Apr-13	13	3060	0	3060	North Star	Missing, Ethiopia
Ağrı	Ad	Jun-13	18	4429	997	3432	Microwave	Missing, Turkey
Tuzluca	Ad	Jun-13	40	23777	12281	11496	Microwave	Missing, Saudi Arabia
Ardahan	Ad	Jun-13	15	8513	4240	4273	Microwave	Missing, Yemen
Logiya	2	Dec-13	36	8422	2330	6092	Microwave	Alive
Mille	2	Dec-13	18	4332	0	4332	North Star	Missing, Ethiopia
Haydi	3	Jun-14	22	4105	1342	2763	North Star	Missing, Kenya
İşte	Ad	Jun-14	30	5581	2640	2941	North Star	Alive
Serhat	Ad	Jun-14	4	828	765	63	DynaTrak	Missing, Ethiopia
Çabuk	2	Jul-14	19	3591	1238	2353	North Star	Missing, Ethiopia
Orada	2	Jul-15	16	1874	906	968	Ecotone	Alive
Armenia	3	Jul-15	3	1161	802	359	Ecotone	Missing, Ethiopia
Goris	Ad	Jul-15	4	845	845	0	Ecotone	Missing, Ethiopia

Table 3.3. Home range sizes (95% Brownian-bridge movement model (BBMM)) of Egyptian vultures by age and season and combined utilization distribution (UD) core-use areas. Home range values are medians, with the inter-quartile range in parentheses. UD contour levels are the area within which 50%, 75%, 95%, 99% of the utilization occurred by the population.

95% BBMM HR Size (km²)		
Age	Summer	Winter
2nd Year	NA	15920 (12920 - 18920)
Third Year	27280 (15990 - 42420)	3791 (2821 - 4760)
Fourth Year	68490 (39380 - 97180)	1838*
Adult Non-breeder	2921 (2084 - 6106)	2082 (453 - 3297)
Adult Breeder	465 (441 - 489)	NA
All	5106 (2071 - 21164)	2333 (1841 - 5124)
UD Size (km²)		
Contour	Summer	Winter
50%	41.68	2.66
75%	96.27	15.08
95%	541.54	184.55
99%	2058.48	1113.58

*only one HR in age class and season

Table 3.4. Standardized coefficient estimates (β), standard errors (SE), and 95% confidence intervals (CI) for covariates used in the final second-order resource selection model of Egyptian vulture space use. A negative β for a “distance-to” (e.g. Dist2Grass) metric indicates selection *for* proximity to that covariate.

Summer				
			95% CI	
	β	SE	Lower	Upper
Intercept	-4.112	0.017	-4.146	-4.078
Dist2Crop	0.300	0.010	0.281	0.319
Dist2Grass	-0.386	0.015	-0.417	-0.356
Dist2Savannah	-0.237	0.011	-0.259	-0.216
Dist2Desert	-0.257	0.017	-0.290	-0.223
GPW	-0.050	0.005	-0.061	-0.040
Dist2City	0.277	0.007	0.263	0.291
Dist2Town	-0.321	0.010	-0.341	-0.302
Dist2Powerline	-0.871	0.015	-0.901	-0.842
Dist2Highway	-1.231	0.018	-1.267	-1.195
Elevation	-0.439	0.011	-0.460	-0.417
Ruggedness	0.172	0.010	0.153	0.191
TreeDensity	-0.126	0.012	-0.150	-0.102
Precipitation	-1.027	0.014	-1.055	-1.000
Winter				
			95% CI	
	β	SE	Lower	Upper
Intercept	-4.985	0.016	-5.016	-4.953
Dist2Forest	-0.446	0.007	-0.459	-0.432
Dist2Grass	-0.685	0.012	-0.709	-0.661
Dist2Desert	-1.866	0.029	-1.922	-1.810
Dist2Town	-0.052	0.006	-0.064	-0.040
Dist2City	0.111	0.007	0.098	0.124
Dist2Powerline	-0.295	0.006	-0.307	-0.284
Dist2Highway	0.209	0.007	0.195	0.222
Elevation	-1.098	0.011	-1.119	-1.077
Ruggedness	0.215	0.006	0.203	0.227
TreeDensity	-0.405	0.024	-0.452	-0.359
Precipitation	-1.244	0.011	-1.265	-1.224

Table 3.5. Status of 27 IBAs identified as being important for Egyptian vultures within our study regions based on observed and predicted use.

Threat Score (Pressure)		Condition Score (State)		Action Score (Response)		EV Trigger Species?	
Assesment	# IBAs	Assesment	# IBAs	Assesment	# IBAs	Assesment	# IBAs
Very High	3	Favourable	1	Low	2	Yes	5
High	3	Unfavourable	3	Negligible	7	No	22
Medium	4	Very Unfavourable	3	Not Assessed	18		
Low	1	Not Assessed	20				
Not Assessed	16						

CHAPTER 4

IDENTIFYING CRITICAL MIGRATORY BOTTLENECKS AND STOPOVER SITES FOR AN ENDANGERED MIGRATORY SOARING BIRD ACROSS THREE CONTINENTS

Buechley, E.R., Opper, S., Beatty, W.S., Nikolov, S.C., Dobrev, V., Arkumarev, V., Saravia, V., Bougain, C., Bounas, D., Kret, E., Skartsi, T., and Şekercioğlu, Ç.H. In Review. Identifying Critical Migratory Bottlenecks and Stopover Sites for an Endangered Migratory Soaring Bird Across Three Continents. *Ecography*.

Abstract

Migrant birds face a number of threats throughout their annual cycle, including habitat change, persecution, collision with energy infrastructure, and climate change. A key challenge for the conservation of migrants is the identification of important habitat, including migratory concentration areas, because species survival rates may be determined by events in geographically very limited areas. While migrant birds differ extensively in their ecology, many species often congregate at the same geographic bottlenecks during migration. Remote-tracking technology is facilitating the identification of such critical habitat, although the strategic identification of important sites and incorporation of such knowledge in conservation planning remains limited. Here we identified 75 complete migration tracks from 45 individuals of an endangered, obligate-soaring migrant (Egyptian vulture, *Neophron percnopterus*), that traversed three continents along the Red Sea Flyway. This flyway is the second most important in the world, yet is perhaps the least studied globally. Egyptian vulture is an obligate soaring migrant and is expected to be an excellent indicator of migratory concentration areas for soaring birds generally. Using dynamic Brownian bridge movement models, we quantified migration paths and use areas to identify the most important migratory bottlenecks and stopover sites on the flyway. These areas each accounted for <5% of the overall movement range of the tracked birds, yet >20% of all tracks passed through the bottlenecks, and >50% of the overall vulture time spent on migration fell within the stopovers. The most important sites were located at the Gulf of Iskenderun (Turkey), the Suez Canal zone (Egypt), and the southeastern Red Sea coast and Bab-el-Mandeb Strait (Saudi Arabia, Yemen, Djibouti). It is discouraging, however, that none of the area within

the major migratory bottlenecks was protected and only <13% of the area within the major stopovers was protected. This demonstrates a very concerning gap in the protected area network for migratory soaring birds along the Red Sea Flyway. Because reducing threats at migratory concentrations can be a very efficient approach to protect populations, our work provides clear guidelines where conservation investment is urgently needed to benefit as many as 37 migratory soaring-bird species, including 8 species at risk of extinction, that regularly use the Red Sea Flyway.

Introduction

Approximately 19% of all bird species are migratory, of which 11% are threatened or near-threatened with extinction (Kirby et al. 2008). Migrant birds face a number of threats throughout their annual cycle, including habitat change, persecution, collision with energy infrastructure, and climate change (Kirby et al. 2008). Conservation of migratory species is particularly challenging, because it may be ineffective if focused solely on one portion of the species' range (Runge et al. 2014). If species concentrate within small geographic areas during migration, impacts at these sites could have population-level effects (Runge et al. 2014). A key challenge for the conservation of migratory birds, then, is the identification of important habitat throughout the annual cycle, including breeding and wintering grounds, as well as migratory stopovers and bottlenecks (Runge et al. 2014, Horns et al. 2016)¹. The increasing availability and miniaturization of remote-tracking technologies is facilitating a boom in the study of the full annual cycles of migratory birds, which allows the identification of such critical

¹Migratory stopovers are areas where individuals rest, feed, or stage during migration. Migratory bottlenecks are areas where multiple individuals concentrate during migration due to geographical, meteorological, or other factors.

habitat (Bridge et al. 2011, Vickery et al. 2014). However, the incorporation of such knowledge in conservation planning remains limited (Runge et al. 2014).

While uniquely challenging, conservation of migratory birds is critically important. Migratory birds perform many valuable ecosystem services (Whelan et al. 2008), such as seed dispersal (Howe and Desteven 1979, Nathan et al. 2008), or control of agricultural pests (Kellermann et al. 2008, Philpott et al. 2009), and thus link spatially disparate ecological communities (Bauer and Hoyer 2014). Detrimental effects that occur at any stage along the flyway and reduce the populations of migratory birds may therefore have ecosystem consequences across continents if migratory birds no longer fulfill their roles in these ecological communities. One guild of birds that has a keystone status (Mills et al. 1993) are scavengers like vultures, as declines in vulture populations can result in trophic cascades and mesopredator release (Buechley and Şekercioğlu 2016a, 2016b) and human rabies epidemics (Markandya et al. 2008). Vultures are the most endangered group of birds, with nine species Critically Endangered, three Endangered, and four Near Threatened (BirdLife International 2017, Buechley and Şekercioğlu 2016a). The long-distance migrations of some vulture species (e.g. García-Ripollés et al. 2010, Mandel et al. 2008) indicate that population declines could have negative consequences for ecosystems across continents connected by migrations.

One of the vulture species that exhibits regular intercontinental migrations is the Egyptian vulture (*Neophron percnopterus*), an obligate scavenger distributed across southern Europe, central and southern Asia, the Middle East and Africa (BirdLife International 2017). In 2007, the Egyptian vulture was uplisted from Least Concern to Endangered due to widespread and sharp population declines, range contractions, and

extinctions of populations caused by inadvertent poisoning, electrocutions, collisions with wind turbines, reduced food availability, and persecution (Cuthbert et al. 2006, Virani et al. 2011, Ogada et al. 2015, Veleviski et al. 2015). The Egyptian vulture has been the focus of considerable research and conservation effort, mostly in Europe (e.g., López-López et al. 2014), and India (e.g. Cuthbert et al. 2006), with some studies illuminating the migration routes and winter ranges of birds breeding in Europe (Buechley et al. In Review, Ceccolini et al. 2009; García-Ripollés et al. 2010; López-López et al. 2014b, Meyburg et al. 2004, Opperl et al. 2015). Nonetheless, little is known about the status and ecology of the species in Central Asia, the Middle East, and North Africa, and there is little information on concentration areas during migration, which hinders conservation planning. Indeed one of the primary recommended actions for future research and conservation of the species is to identify migratory bottlenecks and stopovers, and then work to mitigate threats therein (Dobrev et al. 2015, Opperl et al. 2015).

Furthermore, Egyptian vulture is an excellent model species to identify migratory habitat for soaring birds generally. It is an obligate soaring migrants—meaning that it relies heavily on thermal or orographic uplift to migrate (Bildstein, 2006; Mandel et al., 2008). Their migratory routes are therefore largely shaped by geographic features, and in particular avoidance of water crossings (García-Ripollés et al. 2010, Opperl et al. 2015), which are characteristics shared by many migrants (Bildstein 2006). The species is therefore an excellent indicator of migratory concentration areas for soaring birds generally, as is evidenced by observed congregations of the species at many known migratory bottlenecks (Shirihai and Christie 1992, Welch and Welch 1988).

This study was located at the intersection of Europe, Asia, and Africa, in a region recognized as the Red Sea Flyway (UNDP, 2006). The Red Sea Flyway is the second most important flyway for migratory birds in the world and the most important route for Palearctic birds migrating to and from Africa, yet it is perhaps the least studied major flyway in the world (UNDP, 2006). Well over one million migratory soaring birds of at least thirty-seven species regularly use this flyway, including eight species at risk of extinction (UNDP 2006, Welch and Welch 1988). Nearly the entire world populations of the Critically Endangered Northern Bald Ibis, the Critically Endangered Sociable Lapwing, and Levant Sparrowhawk (*Accipiter brevipes*) concentrate here on migration, as well as >90% of the lesser spotted eagle (*Aquila pomarina*) population, app. 60% of Eurasian honey buzzard (*Pernis apivorus*) and the endangered steppe eagle (*Aquila nipalensis*), and app. 50% of short-toed eagle (*Circaetus gallicus*), booted eagle (*Hieraaetus pennatus*), and white stork (orthern *Ciconia ciconia*) populations (BirdLife International 2017, UNDP 2006). Several of these species are the focus of extensive research and conservation programs in Europe and Asia, yet their trajectories may be limited by threats faced on migration. Furthermore, approximately 50% of the global population of the Egyptian vulture uses the Red Sea Flyway (UNDP 2006), making this arguably the most important region for research and conservation of the species.

We use data from 45 Egyptian vultures that were tracked over a period of eight years (2010-2017) across Eastern Europe, the Middle East and North and East Africa, and that migrated along the Red Sea Flyway (Figure 4.1). Using dynamic Brownian bridge movement models, we quantified migration paths and use areas to identify the most important migratory bottlenecks and stopover sites on the flyway. We then evaluate

the percentage of these key sites that are included in the protected area network and highlight gaps in protection. Because reducing threats at migratory concentrations can be a very efficient approach to protect populations, our work provides clear guidelines where conservation investment is urgently needed to benefit as many as 37 migratory soaring-bird species, including 8 species at risk of extinction, that regularly use the Red Sea Flyway.

Methods

Vulture capture and tagging

From 2010-2016, 45 Egyptian vultures were trapped and fitted with satellite transmitters in Bulgaria, Greece, Turkey, Armenia, Ethiopia, and Djibouti. Tagging in Bulgaria and Greece, hereafter referred to as the “Balkans”, was done by the LIFE+ project “The Return of the Neophron” (LIFE10 NAT/BG/000152). Twenty-nine birds were tagged in the Balkans, the majority of which were juveniles tagged in the nest prior to fledging ($n= 24$). The other five birds were adults: three were captured with a manually-triggered net trap at a feeding site, and two were found poisoned in Greece and were tagged and released after rehabilitation. Tagging in Turkey, Armenia, Ethiopia, and Djibouti, hereafter simplified as “Middle East,” because all of these birds exhibited similar summer and winter ranges, was led by the University of Utah, USA. Sixteen birds were tagged in the Middle East, including seven adults and 9 sub-adults (ages 2-4). All birds in the Middle East were captured near municipal waste dumps, where they reliably congregate (Al Fazari and McGrady 2016) using padded leg-hold traps with weakened springs to minimize the risk of injury (Bloom, 1987). All captured birds were measured, checked for overall health, and were in good physical condition when released. Permits

were acquired for each country and year of capture.

In the Balkans, all birds were fitted with 45g solar-powered Microwave Telemetry GPS transmitters, while birds in the Middle East were tagged with Microwave Telemetry, Ecotone Telemetry, North Star Telemetry, or DynaTrak GPS transmitters. All 45 units were attached as backpacks with 8 mm Teflon[®] ribbon, and can operate continuously for many years because the solar panel is sufficient to re-charge the battery. Transmitters weighed 24-45 g, accounting for <3% of body mass, as recommended (Klaassen et al. 2014). Six transmitters attached in the Middle East used the GSM network to relay GPS fix data. The other 39 units across both tagging regions used the Argos Satellite Data Collection Relay System (CLS America, USA). Two units in the Middle East recorded positions at a temporal resolution of one point per minute; all others recorded positions only up to once per hour. All data were automatically downloaded and incorporated into the Movebank database (www.movebank.org).

Processing GPS telemetry data

Telemetry data were censored to remove erroneous locations using the “longest-consistent track” filter in Movebank (2016). To roughly standardize the temporal resolution of the data across all units, we excluded all but the first location point for each individual in each hour from the two units that recorded data at higher resolution.

Individual-level migration parameters

To identify concentration areas during migration, we first segmented the raw tracking data for each individual to extract those data associated with long-distance

migration. We identified migration parameters (migration start date, end date, duration, and distance) with a method based on net displacement (ND) (Figure 4.2). ND measures the straight line distance between the first location (i.e. the trapping location) and all subsequent relocations for an individual animal (Beatty et al. 2013, Bunnefeld et al. 2011). We calculated daily ND values for each bird with the first relocation recorded each day. We specifically used one point per day because we were interested in broad scale movement patterns to define migration phenology.

We then fit a nonlinear model based on the three-parameter logistic growth model (Pinheiro and Bates 2000) to the ND values for each bird. The migration distance (δ), or the distance of migration between the winter and summer range, varied among migration events to account for individuals that returned to different wintering and/or summering areas each year (Bunnefeld et al 2011). In addition, the migration midpoint (θ), or the point at which half of the migration distance was completed, and scale parameters (φ), or the temporal duration of migration, also varied among migration events to account for heterogeneity in migration patterns among years and seasons. We identified the migration start date as $\theta - 3\varphi$ and the migration end date as $\theta + 3\varphi$ to correspond to approximately 5% and 95% of asymptotic height, respectively. Although previous researchers have used $\theta \pm 2\varphi$ (Beatty et al. 2013) or $\theta \pm \varphi$ (Bunnefeld et al. 2011), the objective of this study was to identify important stopover areas during migration. Consequently, we wanted to liberally define the migration period to include all potential information on bird movements during the migration period.

We conducted further visual inspection of empirical ND data and migration parameters from fitted models to validate migration events (Figure 4.2). Our criterion for

a validated migration event involved a bird moving from traditional wintering grounds to summering grounds or vice versa. We identified numerous immature birds that wandered widely throughout North Africa, which included long distance movements during the migratory season. We identified such forays as nonmigratory movements and excluded them from further analyses. In addition, we identified several vultures that initiated a migration event, but did not complete the migration event. For these individuals, we only made inferences on migration start date. We performed all operations in R, using the `nls` function (R Core Team 2017) and the `adehabitatLT` package (Calenge 2013).

Identifying migratory stopovers and bottlenecks

Egyptian vultures are diurnal soaring migrants that rest frequently during migration. At the population level, the areas that would be most important for conservation activities are those where one or more individuals spend a lot of time during migration (stopover sites) or where multiple individuals migrate through a relatively narrow area where they may be exposed to certain threats (bottlenecks). We used dynamic Brownian bridge movement models to analyze space use and corridors during migration, which allowed us to quantify the use of geographic areas by the tracked population. The Brownian bridge movement model is based on a probabilistic model of the movement path between relocations (Horne et al. 2007). This model uses the time between successive points, the uncertainty inherent in the location coordinates, and an uncertainty component that describes how much the animal's trajectory deviated from a straight-line movement (Brownian motion variance, σ_m^2), within a random walk framework to estimate the probability of use of a given geographic area (Horne et al.,

2007). The Brownian bridge movement model is particularly useful for delineating migration tracks of animals because it produces a probabilistic estimate of the path of migration between points, and facilitates identification of sites used as stopovers and migration corridors (Fischer et al. 2013, Sawyer et al. 2009).

The *dynamic* Brownian bridge movement model (dBBMM), which we use here, is a further refinement of the Brownian bridge movement model that identifies distinct movement patterns (e.g. active migration versus stopover) and assigns a variable Brownian motion variance along the movement path given that an animal's behavior varies predictably between distinct patterns (Kranstauber et al. 2012). This classification is accomplished by searching over temporal “windows” of the data to identify changes in the amount of displacement between points. The dBBMM accurately distinguishes between stopover sites with local movements and long-distance movement corridors, and is thus ideal for evaluating avian migrations for species that do not fly nonstop such as diurnal soaring raptors (Palm et al. 2015). The output of the dBBMM is a utilization distribution (UD), which summarizes the area and relative intensity of use (Worton, 1989). We used the UDs resulting from the dBBMM to identify migration stopover sites and bottlenecks throughout the study area.

We used the migration start and end dates as identified from the individual-level net displacement models (including all points from the first and last day of each migration segment) and calculated UDs for each individual and migration based on the dBBMM in the *move* package (Kranstauber and Smolla 2015) in R. We set the grid size for all UD calculations to a 10km² resolution, which provided relatively high resolution mapping over the very large extent of Egyptian vulture migrations (across 3 continents),

while maintaining computational efficiency. We set the window size and margin, which control the Brownian motion variance parameter, and which must be odd numbers, at 25 and 9 subsequent hourly locations, respectively, which corresponded to a window size of approximately one day (Kranstauber et al. 2012, Palm et al. 2015). This choice was based on the biological rhythm of a diurnal soaring migrant such as the Egyptian vulture, where daily movements are interspersed by nocturnal rest periods of ~8 hours, and these window and margin sizes should thus identify changes in σ_m^2 both within and across days over the course of each migration trajectory.

To identify migratory stopover sites, we weighted each individual UD by the migration duration, by multiplying all pixels in the UD by the number of days spent on that migration trajectory (Palm et al. 2015). This effectively converted the proportional UD to a common currency (number of days) that could be used across migratory journeys of different duration. We then summed all individual UDs to create a global UD for all tracked individuals over the entire study area, and normalized it so that the cumulative pixel values summed to 1 (Palm et al. 2015, Sawyer et al. 2009). The resulting UD provided an estimate of the proportional use of each 10km² grid cell by all tracked individuals over the entire study area. We then identified the 50%, 75%, and 99% probability densities (i.e. the smallest area within which EV spent $x\%$ of time) of the UD. Following Palm et al., (2015), we assumed that the 50% probability were high use areas and the 75% probability were moderate use areas. The 99% probability effectively represents the range map for all Egyptian vultures tracked in this study.

To identify migratory bottlenecks, we summed the number of migration routes—as identified from the 99% probability densities for each individual migration

trajectory—that overlapped in each 10km² grid cell over the entire study area (Sawyer et al. 2009). We then divided this by the total number of migration routes in the study to produce a raster where each cell had a value indicating the proportion of all migration tracks that passed through it. As many as 35% of all migration tracks intersected any given 10km² grid cell. We assumed that areas with 10-20% of migratory paths were migration corridors (of medium importance), and >20% were migration bottlenecks (of high importance). While >20% intersection may not seem a high cutoff for a “bottleneck,” note that this represents migration tracks from Egyptian vultures tagged across 6 countries and three continents intersecting a relatively tiny 10km² grid cell. To visualize how migratory bottlenecks differed between seasons, we subset the data by season and repeated the above processes.

We used all migration paths in both stopover and bottleneck analyses, including those of incomplete migrations (e.g., when a bird died on migration), because we deem all trajectories to contribute important information about the migration ecology of the species. Furthermore, 16 of 45 birds were tracked for more than one migration event and each migration trajectory was included because many birds used different migration paths between seasons and years. However, although individuals contributed up to seven migration trajectories, this constituted just 7.7% of all migration tracks, and no individual had an overly large influence on the location of stopover sites or bottlenecks.

Conservation gaps and priorities

Because the inadequate protection of important migration routes is a recognized deficiency for long-distance migrants (Runge et al. 2014), we calculated the area and

percentage of Egyptian vulture use areas that fell within existing protected or recognized areas of importance. In this analysis, we included both protected areas (PAs) in The World Database of Protected Areas (IUCN and UNEP-WCMC, 2012), obtained from protectedplanet.net (Feb. 22, 2017), and Important Bird Areas (IBAs) (BirdLife International 2017). The PA database includes sites that are designated or proposed nationally and under regional and international agreements (IUCN and UNEP-WCMC 2012). IBAs are recognized for their importance for birds, but do not provide any formal protection unless they are inscribed as protected areas in national legislation (BirdLife International 2017).

Results

Individual-level migration parameters

Two birds from the Balkans died prior to migrating and two birds tagged in Ethiopia and Djibouti never migrated out of Africa. Of the 41 remaining migratory individuals, there were 22 juveniles, 7 sub-adults (2nd through 4th years) and 12 adults. Individual-level net displacement models identified 75 complete migration events, and 17 incomplete events. Incomplete migration events were associated with either mortality or transmitter failure during migration. Of the 41 individuals, twenty-three were tracked for just one migration event; two were tracked for two migrations, ten for three, three for five, one for six, and two for seven. Because Egyptian vultures aged over the course of the study, our sample included 22 juvenile (1st year), 25 immature (2nd-4th years), and 41 adult (5+ years) migration events.

Migratory stopovers and bottlenecks

Egyptian vultures tracked in this study had a large range (99% probability UD) across Eastern Europe, the Middle East, and North and East Africa, encompassing nearly four million km² (Figure 4.3). Moderate use areas (75% probability UD) were mainly concentrated along the eastern Mediterranean and Red Sea coasts. High use areas (50% probability UD) were highly concentrated along the southeastern Red Sea coast (Saudi Arabia and Yemen), the Sinai Peninsula (Egypt), and the Bosphorus Strait (Turkey). High use areas encompassed just 4.7% of the overall range. Most birds did not spend more than a night at any given stopover site, and therefore the high use areas primarily represent sites that were used by many individuals during migration.

Similarly, migration corridors (areas with between 10% and 20% of migration tracks) were concentrated along the eastern Mediterranean and Red Sea coasts (Figure 4.4). Migration bottlenecks (areas with >20% of migration tracks) were very concentrated in a very small area representing just 0.6% of the overall range, and were located at the Gulf of Iskenderun (Turkey), the Suez Canal zone (Egypt), and the southeastern Red Sea coast and Bab-el-Mandeb Strait (Saudi Arabia, Yemen, Djibouti). There was a striking difference in the bottlenecks between spring and autumn, with the major bottlenecks located along the southeastern Red Sea coast (Saudi Arabia and Yemen) in autumn, and the northwestern Red Sea coast (Egypt and Israel) in spring (Figure 4.5).

Conservation gaps and priorities

Overall, 9.3% of the entire range of the tracked Egyptian vultures in this study (99% probability UD) was in protected areas (Table 4.1). A higher proportion of

moderate (11.7%) and high-use areas (12.6%) were in protected areas, indicating that Egyptian vultures are disproportionately utilizing the protected area network during migration. However, only 8.3% of migration corridors (10-20% of migration paths) and none (0.0%) of the migration bottlenecks (>20% migration paths) fell within protected areas, demonstrating an important shortcoming in the protected area network for migratory soaring birds along the Red Sea Flyway. Important Bird Areas (IBAs), which are recognized for their importance but do not receive any formal protection, covered an additional 6.7% of high-use areas and 13.1% of migration bottlenecks, and could provide a framework for increasing protection of migratory birds along the Red Sea Flyway (see Table 4.1).

Discussion

Our approach identified key migration concentration areas along the Red Sea Flyway, and revealed that only a very small proportion (<13%) of these important areas are currently protected. We also showed that Egyptian vultures migrating through those concentration areas disperse over very large breeding and nonbreeding ranges across Europe, Asia, and Africa, and that conservation management in these relatively small migration concentration areas could have a very large effect on migratory soaring birds and the ecosystem services they provide across three continents.

Migratory stopovers and bottlenecks

We quantitatively identified migratory stopover sites and bottlenecks (Figures 4.3 and 4.4). Migratory stopovers provide valuable information on where Egyptian vultures

staged during migration, and were more dispersed over the study region than bottlenecks. However, migratory stopovers (Figure 4.3) overlapped extensively with migratory bottlenecks (Figure 4.4), because most birds did not rest for extended periods on migration, and areas where multiple migrations passed through a small area showed up as relatively high use. Migrants can be exposed to anthropogenic threats even in areas where they do not rest or forage, for example through collision with wind turbines or power lines, or through direct persecution, which is rampant around the eastern Mediterranean (Brochet et al. 2016). Thus, targeted conservation actions within relatively small areas could be highly effective if threats to soaring migratory birds can be reduced or eliminated in those areas.

The most important migratory bottlenecks identified in this study are situated in three main areas: 1) the southeastern Red Sea coast including the Bab-el-Mandeb Strait (Saudi Arabia, Yemen, Djibouti), 2) the northern tip of the Gulf of Suez (Egypt), and 3) the eastern corner of the Gulf of Iskenderun (Turkey) (Figure 4.4). Additional important migratory corridors occur at the Bosphorus and Dardanelles straits (Turkey) and in central and northern Jordan. Not all of these areas were used equally during spring and autumn migration: migration bottlenecks occurred at geographic barriers where birds encountered a water barrier they were unwilling to cross (Agostini et al. 2015). These geographic barriers funneled birds to different areas in spring and autumn. For example, the Egyptian vulture population in the Middle East exhibited a clockwise migration strategy where most individuals migrated southwest in the autumn through the Arabian Peninsula until they encountered the Red Sea coast, which they followed south until they crossed into Africa via the narrow Strait of Bab-el-Mandeb. In spring, the same birds typically

migrated northeast, and followed the opposite shore of the Red Sea via North Africa and the Sinai Peninsula (although some birds also returned via Bab-el-Mandeb in the spring). This behavior led to strong geographic differentiation between the migratory bottlenecks and corridors between spring and autumn. Migratory bottlenecks in spring were located along the western Red Sea coast, the Sinai Peninsula, southern Israel, and northern Jordan / southern Syria, whereas in autumn, the major bottlenecks were located along the eastern Red Sea coast, the Strait of Bab-el-Mandeb, and the Gulf of Iskenderun (Figure 4.4). Whether the different route choice is a consequence of the visual navigation process via landlines (e.g., the Red Sea coast), or whether typical wind patterns over the Sahara and the Arabian peninsula make this clockwise migration strategy more efficient will require additional research (Vansteelant et al. 2017).

Conservation prioritization

By overlapping existing protected areas (PAs) and Important Bird Areas (IBAs) with migration stopovers and bottlenecks, we identified conservation gaps for the species during migration. Overall, only 11.7% of moderate use and 12.6% of high use areas during migration fell within the protected area network. But, as compared to 9.3% protection across the entire range, this indicates at least some level of focused protection of these important stopover sites. Discouragingly however, none of the area within migratory bottlenecks and only 8.1% of the area within migratory corridors was protected (Table 4.1). This demonstrates a very concerning gap in the protected area network for Egyptian vultures, as well as the numerous other soaring birds that utilize the Red Sea Flyway and that are known to concentrate at bottlenecks with the Egyptian vulture (e.g.,

Hilgerloh et al. 2011, Oppel et al. 2014, Welch and Welch 1989).

In addition to those areas that fall within the protected area network, Important Bird Areas (IBAs) recognize an additional 6.7% of high use areas, 6.0% of migratory corridors, and 13.1% of migratory bottlenecks for their importance to birds (Table 4.1). However, IBAs in Central Asia, the Middle east and North and East Africa are in particularly dire conditions, with the majority having high to very high threat scores and unfavorable to very unfavorable conditions, and with low to negligible conservation actions taking place (BirdLife International 2017, Buechley et al. In Review, Horns et al. 2016). While IBAs are not formally protected, the IBA network along the Red Sea Flyway could provide a platform by which to conserve migratory birds if measures are taken to officially protect these sites. However, simply designating areas as protected does not guarantee protection or effective conservation measures either (Leverington et al. 2010). For effective conservation of the Egyptian vulture and other migratory soaring birds along the Red Sea Flyway, we encourage increased support for conservation efforts in migratory stopovers and bottlenecks. Our quantitative determination of migratory bottlenecks corroborates extensive evidence on the importance of certain sites for migratory soaring birds, and underscores the importance of conducting research, monitoring and conservation for soaring migrants at three sites in particular: 1) the southeastern Red Sea coast and the Bab-el-Mandeb Strait (Welch and Welch 1988), 2) the Suez Canal zone (Hilgerloh et al. 2011), and 3) the Gulf of Iskenderun (Oppel et al. 2014, Sutherland and Brooks 1981).

As a first step, we recommend initiation and/or continuation of migration monitoring at these major bottlenecks. Counts of birds at migratory bottlenecks can

provide information on the populations and trends of species, and are particularly valuable in areas where information on the breeding and/or wintering populations is sparse (Dunn and Hussell 1995), which is the case for most species using the Red Sea Flyway (UNDP 2006). Observations at the migratory bottlenecks identified here may provide the best means of estimating and monitoring populations of the Egyptian vulture, and could inform the status of the 36 other species of migratory soaring bird, including 8 species at-risk of extinction, that regularly use the Red Sea Flyway. Furthermore, presence of ornithologists at migratory concentrations can help to identify and mitigate threats to species at these sites.

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Table 4.1. Summary of the total area (km²) of Egyptian vulture use areas, and the percentage of each use category that fell within protected areas (PAs) and Important Bird Areas (IBAs). “PAs + IBAs” shows the total area within both PAs and IBAs. “Low use” is the 99% probability utilization distribution (UD), “moderate use” is the 75% probability UD, and “high use” is the 50% probability UD. “Migration corridors” include areas where 10–20% of all migration paths intersected, and “migration bottlenecks” include areas where >20% migration paths intersected.

Layer	Total Area	% PAs	% IBAs	PAs + IBAs
Low use	3,754,800	9.3%	4.4%	13.7%
Moderate use	689,200	11.7%	5.9%	17.6%
High use	177,800	12.6%	6.7%	19.2%
Migration corridors	124,600	8.1%	6.0%	14.1%
Migration bottlenecks	23,100	0.0%	13.1%	13.1%

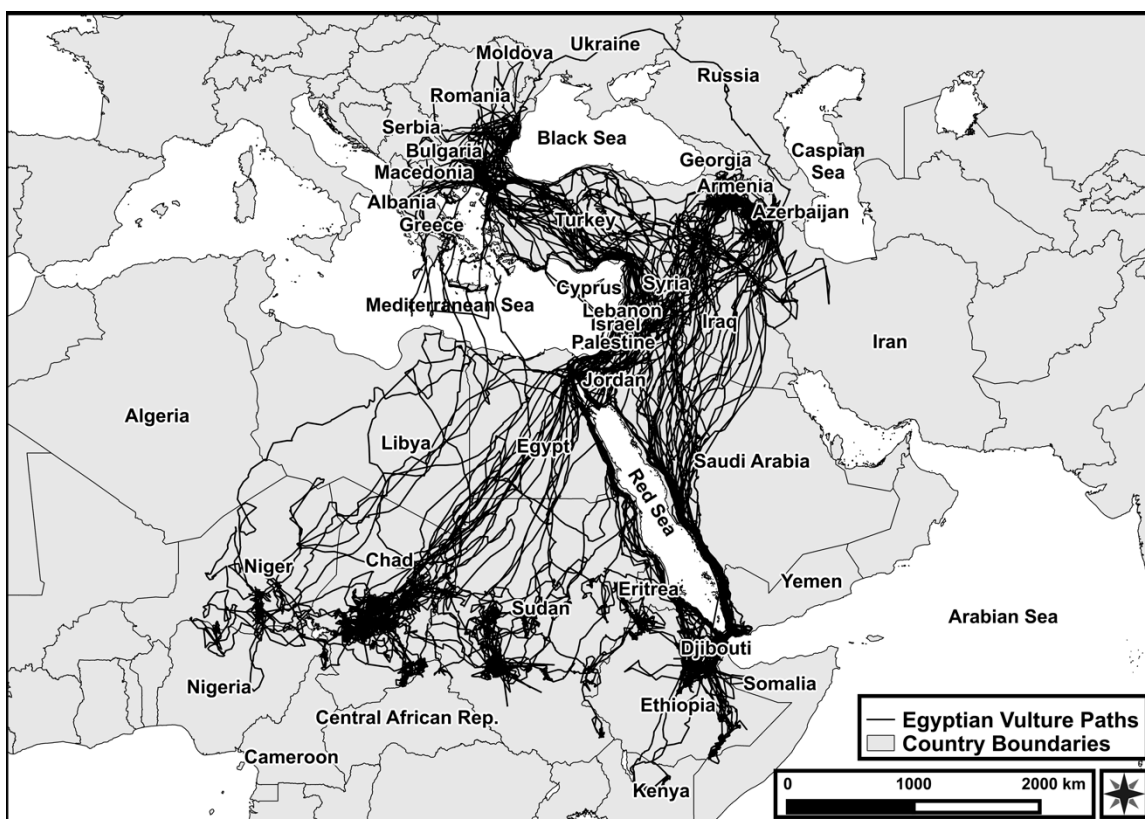


Figure 4.1. Overview map for 75 complete migration events from 45 Egyptian vultures across Eastern Europe, the Middle East, and North and East Africa, along the Red Sea Flyway. All labeled countries were visited by tagged individuals ($n=38$).

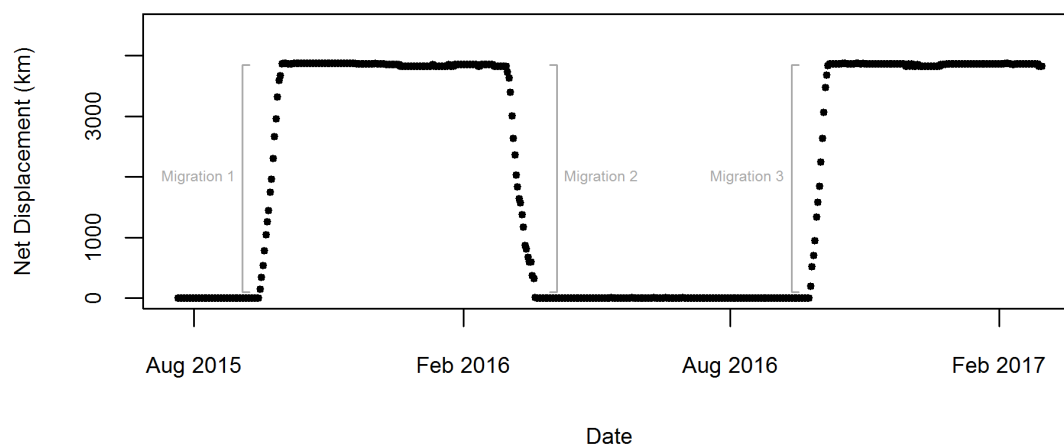


Figure 4.2. Example plot of empirical net displacement values from an adult Egyptian vulture that was monitored from August 2015 to February 2017. Breeding and nonbreeding ranges for this individual are approximately 3,500 km apart and connected via regular, seasonal migrations.

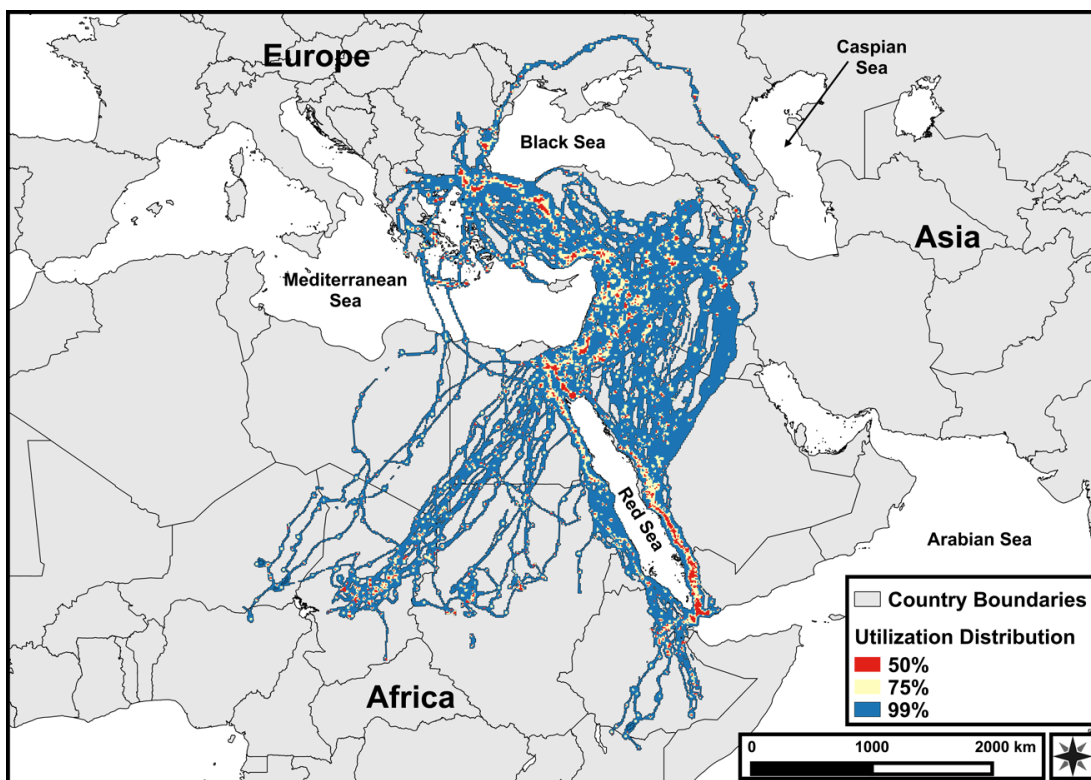


Figure 4.3. Utilization distributions (UDs) for all individuals in the study. Blue indicates low use areas (99% probability UD), yellow indicates moderate use areas (75% probability UD), and red indicates high use areas (50% probability UD).

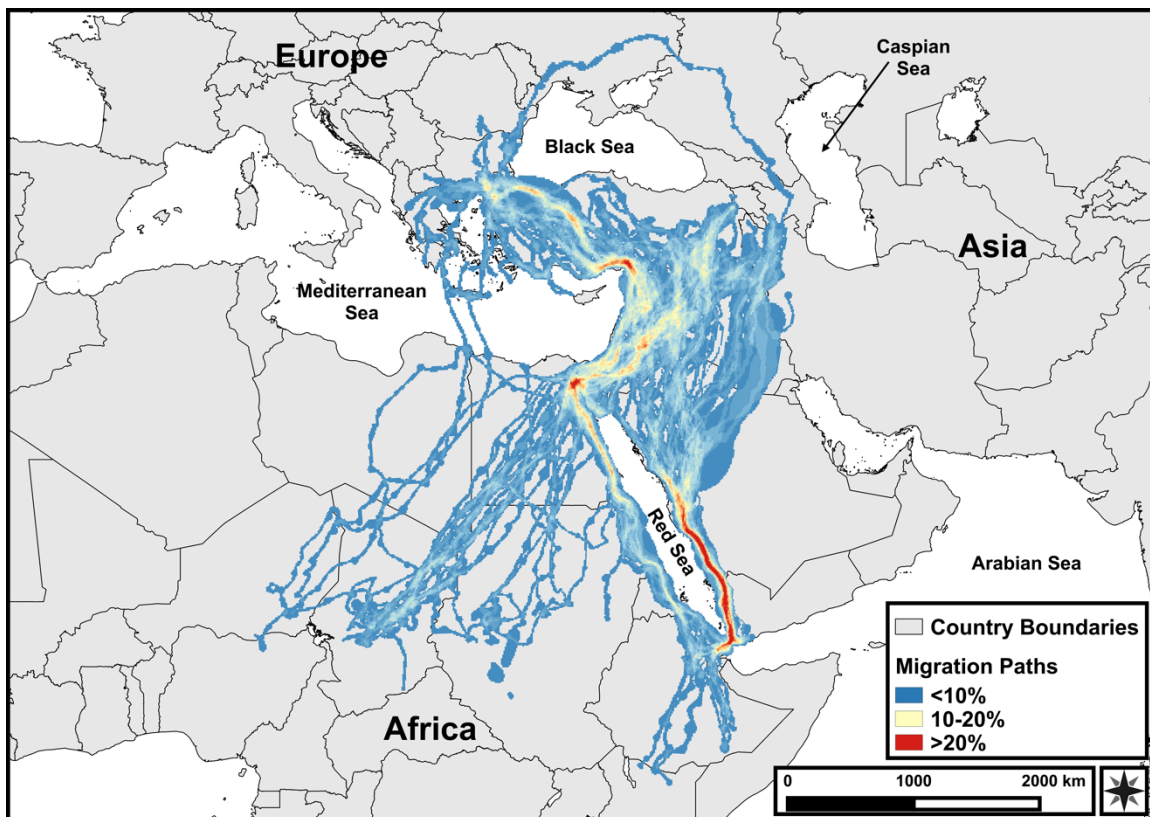


Figure 4.4. An overview of migration paths (areas with <10% of all migration paths), corridors (10-20% of all migration paths), and bottlenecks (>20% all migration paths) for all individuals and seasons.

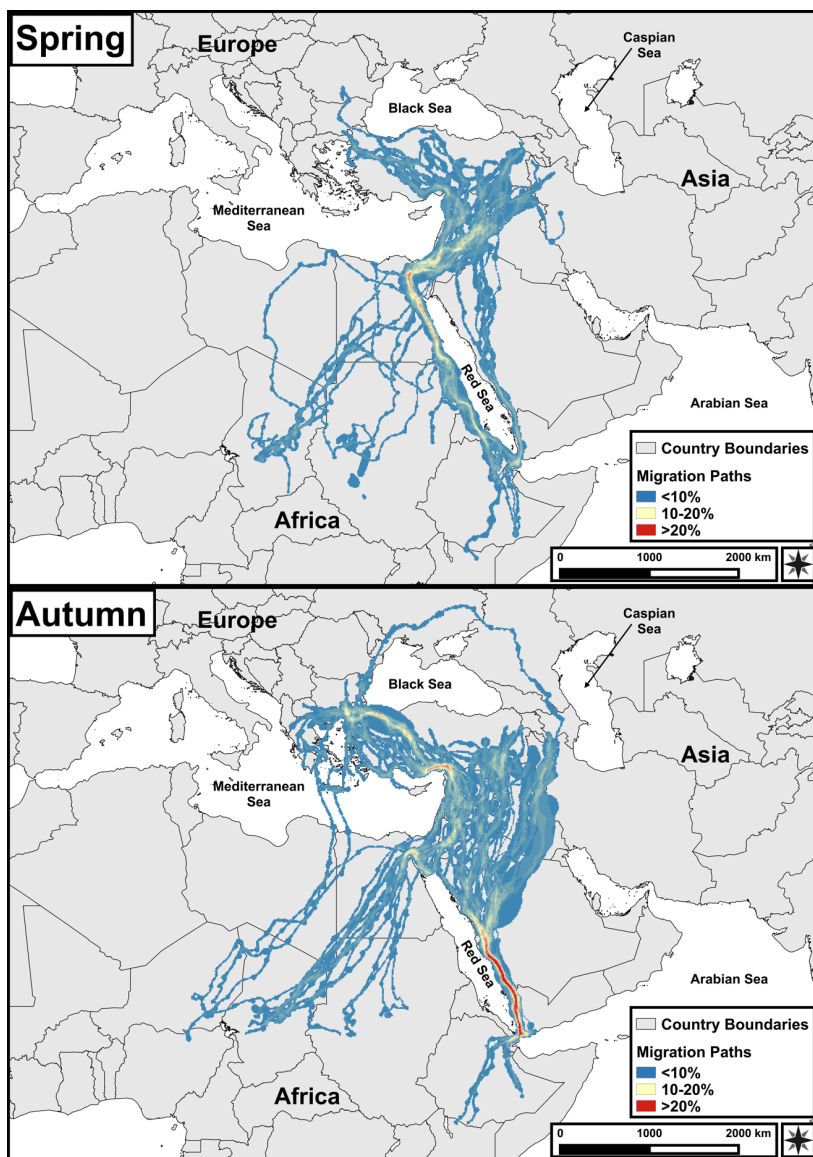


Figure 4.5. An overview of migration paths (areas with <10% of all migration paths), corridors (10-20% of all migration paths), and bottlenecks (>20% all migration paths) for all individuals in the study, split between spring and autumn seasons. Note the very different migratory bottlenecks between the two seasons.

APPENDIX A

ENDANGERED SPECIES

Buechley, E.R. and Şekerciöđlu, C.H. (2003). *Grzimek's animal life encyclopedia*.

Detroit: Gale.



Endangered species

As human populations have increased dramatically over the last few hundred years, mirrored by similarly expanding pressures on the natural world, a strong movement concerned with the well-being of nature has grown in response. At its core, this environmental movement seeks to promote the sustainable harvest of natural resources, to preserve natural landscapes, and to protect biological diversity. Integral to these central principles is the preservation of species, for species provide humanity with renewable natural resources, shape and animate natural landscapes, and bind together complex natural systems. This entry critically reviews the early twenty-first-century status of the endangered species concept, with particular emphasis on the role and realized contribution of the U.S. Endangered Species Act to the management of endangered species. It further provides a brief review of international legislation dealing with endangered species and summarizes the current global status of species.

What is an endangered species?

An endangered species is defined as any species of organism that faces a high risk of extinction within a portion or the entirety of its geographic range. The endangered species concept, however, is a human construct subject to debate and interpretation. Many organizations use varying criteria to determine what merits listing a species as endangered. The most widely recognized of these organizations are the International Union for Conservation of Nature (IUCN) and the U.S. Fish and Wildlife Service (USFWS).

The IUCN Red List of Threatened Species (IUCN 2013b) strives to provide status reports for all species of organisms worldwide, categorizing them into the following nine groups: extinct, extinct in the wild, critically endangered, endangered, vulnerable, near threatened, least concern, data deficient, and not evaluated. Whereas the categories of extinct, extinct in the wild, data deficient, and not evaluated are self-explanatory, the other five categories are more nuanced. A species is listed as critically endangered when it is deemed to face an “extremely high risk of extinction in the wild,” endangered when it is “facing a very high risk of extinction in the wild,” vulnerable when it is “facing a high risk of extinction in the wild,” near threatened when it is “likely to qualify for a threatened category in the near future,” and least concern when the species’ status

does not qualify it for any of the other categories (IUCN 2001 p. 14–15).

In contrast, the USFWS classifies species into only two categories: endangered and threatened. A species is defined as endangered when it is “in danger of extinction within the foreseeable future throughout all or a significant portion of its range” and threatened when it is “likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range” (USFWS 2013a).

While these definitions sound rather simple, there are complications in applying them to real-life scenarios. In all of these definitions there is room for the interpretation of phrases such as “high risk,” “foreseeable future,” and “significant portion.” Further, most species worldwide have not been the subjects of much scientific investigation, making it difficult to assess their status on the basis of evidence. There has been much debate as to whether researchers should assume the worst- or best-case scenario when scientific data are limited: Conservationists often argue the former, but existing policies tend to favor the latter. Even for well-studied species it has proven exceedingly difficult for biologists to predict extinction risk as there are countless factors that can contribute to the decline of a species. In the attempt to calculate the risk of extinction experienced by different species, biologists have established a new subdiscipline of ecology focused on determining minimum viable populations and conducting population viability analysis (Akçakaya and Sjögren-Gulve 2000). Biologists who work in this field attempt to determine the number of minimum populations necessary for a species’ survival and use complex mathematical modeling to estimate the likelihood that these populations will survive over a given period of time under different scenarios. These studies have greatly increased scientists’ understanding of certain organisms and processes, but much work remains in order to decipher the complexity of ecological systems and understand the factors contributing to the decline of species.

Although listing procedures are supposed to be based solely on the best available science, other human interests and biases also influence the listing process. The IUCN and the USFWS are subject to political pressures, and their decisions to list a species may be swayed by social and economic considerations. The existence of other governmental

Endangered species

regulations also factor into the listing process: The USFWS is likely to conclude that species that are provided oversight by other legislation (e.g., marine fish species whose harvest is regulated under the Magnuson–Stevens Fishery Conservation and Management Act) do not necessitate listing under the Endangered Species Act. In addition, listings are subject to aesthetic judgments made by people: Large, charismatic, highly visible, and terrestrial species have typically been more prone to being listed. As the protection, conservation, and rehabilitation of species requires significant time, interest, and resources, it is perhaps inevitable that listing procedures incorporate human interests. Although the definition of what constitutes an endangered species may seem simple, the application of this definition to real-life scenarios has proven exceedingly complex and will likely continue to be so in the foreseeable future.

The importance of maintaining biodiversity

While the decline of species worldwide is indisputable, debates exist about the importance of maintaining biodiversity. Should environmental conservation get in the way of human interests such as economic development, recreation, and comfort? Are extinctions, including mass extinction events, not a natural process? Are human interests and environmental conservation at odds with one another?

Extinctions

Although extinctions have occurred throughout history, there is alarming concern among biologists that the current rate of extinctions is on par with the fastest declines of biodiversity the planet has ever seen. The exact rate of current extinctions is difficult to quantify, however, there is consensus that the rate has been accelerating rapidly as the direct result of human alterations to the global environment. In a contribution to the 1988 book *Biodiversity*, Edward O. Wilson argues that “the current reduction of diversity seems destined to approach that of the great natural catastrophes at the end of the Paleozoic and Mesozoic eras—in other words, the most extreme in the past 65 million years” (11–12).

In an article published in 2000, Stephen Jay Gould addressed the argument that extinctions comprise a natural process and therefore are not of concern. He yielded the points sometimes argued by those who seek to devalue extinctions—that extinctions are unavoidable and that Earth has shown the ability to rebound in terms of biological diversity after mass extinction events. Gould argued, however, that the time scale is important to consider here: Recovery from mass extinctions—that is, the reestablishment of a balance of similar biological diversity—takes millions of years. According to Gould, *Homo sapiens* as a species is thought to be only 200,000 years old, and so:

Of what conceivable significance to us is the prospect of recovery from mass extinction 10 million years down the road if our entire species, not to mention our personal lineage, has so little prospect of surviving that long? Capacity for recovery at geologic scales has no bearing whatever upon the meaning of extinction today. . . . We are trying to preserve populations and environments because

Extinction

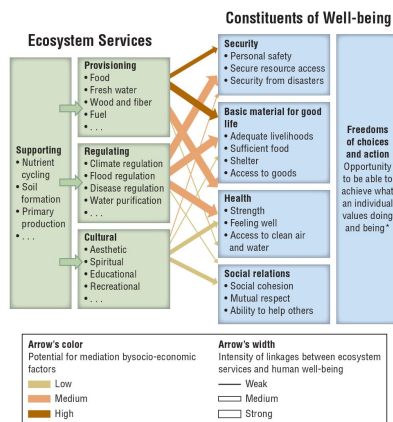
the comfort and decency of our present lives, and those of fellow species that share our planet, depend upon such stability. (232)

He concludes that to say that humanity should let a species go extinct “because all species eventually die makes about as much sense as arguing that we shouldn’t treat an easily curable childhood infection because all humans are ultimately and inevitably mortal” (232).

Ecosystem services

In the attempt to quantify the value of nature to humanity, biologists and environmental scientists have begun to calculate the economic value of natural services (Sekercioglu 2010; Wenny et al. 2011). The study of ecosystem services has grown in popularity over the last several decades and has begun to alter how people think about national and global economies. In a 2000 contribution, Janet N. Abramovitz argued that

nature’s “free” services form the invisible foundation that supports our societies and economies. We rely on the oceans to provide abundant fish, on forests for wood and new medicines, on insects to pollinate our crops, on birds and frogs to keep pests in check, and on rivers to supply clean water. We expect that when we need timber we can harvest it, that when we need new crops we can find them in nature, that when we drill a well we will find water, that the waste we generate will disappear, that clean air will blow in to refresh our cities, and that the climate will be stable and predictable. Nature’s services have always been there free for the taking, and our expectations—and economies—are based on the premise that they always will be. (331–332)



The ecosystem services agenda: bridging the worlds of natural science and economics, conservation and development, and public and private policy. Reproduced by permission of Gale, a part of Cengage Learning.

Extinction

Nature has long been viewed as a boundless resource, and humanity's economies are largely based on this notion. However, current human populations and levels of resource consumption have proven this assumption wrong. Humanity's mechanisms for monitoring the economic success of a nation, such as the US gross domestic product (GDP), deem positive for the economy the blanket consumption of natural resources and do not incorporate the services provided by nature. Abramovitz argued that this encouragement of consumption has led to a "biodiversity deficit," which she defined as the destruction of species and ecosystems faster than nature can create new ones.

Nature's living library—the genes, species, populations, communities, and ecosystems in existence today—represent a wealth of options for future generations and for change in the biosphere. . . . By reducing the number of species and the size and integrity of ecosystems, we are also reducing nature's capacity to evolve and create new life. In just a few centuries we have gone from living off nature's interest to spending down the capital that has accumulated over millions of years of evolution, as well as diminishing the capacity of nature to create new capital. (333)

Whereas Abramovitz focused on the maintenance of current ecosystem services, many other scientists have argued that there are tremendous resources in the natural world that remain to be developed and that could greatly benefit future human civilizations. Wilson stated that "we have come to depend on less than 1% of living species for our existence, the remainder remaining untested and fallow" (1988, 15). There are numerous potential plant sources for food, pharmaceuticals, fibers, and energy sources. Insects may serve as superior crop pollinators and control agents for weeds and pests. Bacteria, yeasts, and other microorganisms have potential as medicines and food, as well as in soil restoration and toxic waste remediation. In summary, nature has the potential of providing a diverse array of solutions to human problems. Humanity has only begun to explore and tap into these resources, while simultaneously destroying them at a rapid rate.

Ethics

Although it is important to consider human self-interests as a species in regard to the natural environment, including the analysis of ecosystem services provided to humans by nature, some argue that humanity has a moral and even religious commitment to maintaining biodiversity and ecosystem integrity. In a 2004 contribution, Holmes Rolston III stated that "the motivation to save endangered species can and ought to be pragmatic, economic, political, and scientific; deeper down it is moral, philosophical, and religious" (233).

In what is regarded as one of the classic essays in conservation literature, "The Land Ethic" (originally published in 1949), Aldo Leopold wrote the following: "A system of conservation based solely on economic self-interest is hopelessly lopsided. It tends to ignore, and thus to eventually eliminate, many elements in the land community that lack commercial value, but that are (as far as we know) essential for its healthy functioning. It assumes, falsely, I think, that the

Endangered species

economic parts of the biotic clock will function without the uneconomic parts" (2004, 378).

Leopold argued that people have a duty to attempt to conserve all of the parts of the "clock," his metaphor for the natural world, as every component is important when united, even though they may not be valuable independent of the other pieces. He went on to state that "health is the capacity for self-renewal. Conservation is our effort to understand and preserve this capacity" (381). Leopold summarized his land ethic in this now-famous statement: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise" (382). Modern ecological thought provided support for Leopold's ethic, with findings that small, overlooked, and even seemingly bothersome species play important roles in the maintenance of ecosystems. For example, in a 2003 contribution, Svata M. Louda and Tatyana A. Rand argued that

there are practical as well as aesthetic and ethical reasons for working to maintain minor, even seemingly obnoxious, species and their interactions. In particular, this case suggests that we are not yet in a position to predict the cost associated with the decline and loss of a specific species, since its ecological function and economic value may not be obvious. (6)

While Leopold's land ethic argues for conservation for the inherent good of nature, other authors have argued that there is a more spiritual and/or religious basis for the need for conservation. In a 2002 contribution, Stephen R. Kellert contended that the conservation of nature should be based not on pity for the weak, but on our own self-interest. He argues that nature enhances humanity's capacity for experiencing beauty and fulfillment in our lives and for feeling connected to something greater than ourselves: "a broad anthropocentric ethic of duty and responsibility for the natural world reaffirms our complicated and unyielding ties with creation. We draw ethical nourishment and moral guidance from recognizing and celebrating this commonality. Conversely, degrading our relation with nature engenders more than material harm. It leads, far more profoundly, to a loss of identity, meaning, and purpose" (64). In a more overtly religious argument, Rolston highlights the story of Noah's Ark as an example of how "God wills for each species on Earth to continue, despite the disruptions introduced by humans" (233).

The rise of human culpability

Human populations have likely been responsible for the extinction of species for millennia. The extinction of megafauna in Asia, Europe, Oceania, and the Americas parallels the arrival of ancestral humans to these continents in their emigration from Africa thousands of years ago, and although there is little direct evidence of human involvement in these extinctions, there are well-argued theories suggesting this to be the case (Martin 2005; Presscot et al. 2012). The development of tools, including the use of fire and hurling rocks and the crafting of spears and bows, allowed for the easy capture of unsuspecting animals. Human intelligence allowed for human populations to grow, as prey species declined and

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became extinct around the globe. Undoubtedly some early cultures became aware of their impacts and perhaps sought a balance with prey species in order to preserve these resources. Many early civilizations found some degree of balance with their natural surroundings.

As human global mobility increased drastically in the second millennium AD with the development of oceangoing craft able to navigate oceans and as peoples from one continent began harvesting resources from another, the human–nature balance was disturbed. In particular, islands, as relatively small and vulnerable tracts of land, were drastically affected by the new arrivals of humans, whether the islands were previously inhabited or not. From the fifteenth to nineteenth centuries, islands experienced a new and devastating wave of extinctions. These extinctions occurred rapidly and, for the first time, were documented extensively (Pimm et al. 2006). The pattern of extinctions was most obvious among birds, as they were more easily observed than other taxa. A 2012 paper by researchers at BirdLife International and Charles Darwin University summarized the bird extinctions from 1500 until the early 2000s, citing the extinction of 279 species and subspecies of birds (Szabo et al. 2012). According to this research, the majority of these extinctions have taken place on oceanic islands, with 78.7 percent of species extinctions and 63 percent of subspecies extinctions. For example, Hawaii lost 36 species and subspecies, the tiny archipelago of the Mascarene Islands in the Indian Ocean lost 27, New Zealand lost 22, and French Polynesia 19. Alarming, this study finds that the rate of bird species extinctions is now accelerating on continents.

One particularly important and noteworthy case of extinction was that of the dodo (*Rapbus cucullatus*) on the island of Mauritius in the Indian Ocean. European explorers first discovered the island in 1507. Starting in 1598, the island became a frequent stopover for Dutch traders crossing the Indian Ocean. The first record of people eating dodos comes from 1601. Though not regarded as particularly tasty, the large, flightless and naive birds were hunted easily and fed many people. Records from early sailors show that the dodos were harvested by the dozen. Further, exotic pigs, monkeys, goats, chickens, cattle, deer, cats, and dogs were all introduced to the island by the early visitors; pigs and monkeys became direct predators of dodos, and other introduced species competed with them indirectly. With all of these pressures, the species declined rapidly. The last sighting of the dodo was made on the island of Mauritius in 1662 (Quammen 1996).

The decline of the dodo was so precipitous and undeniably caused by human influences on the island that it became a famous example of the impacts of early explorers on island ecology. Environmental historians often characterize this episode as being instrumental in the awakening of human awareness of how people can affect ecosystems. People began to realize that resources could be exhausted and that humans could completely eradicate a species from Earth in a relatively short amount of time. It could be argued that the endangered species concept has its roots in this episode in the mid-seventeenth century.

Although the seed of responsibility may have been planted in the human psyche in the seventeenth century, it took a few

Extinction



Illustration of the extinct Steller's sea cow (*Hydrodamalis gigas*), a sirenian that lived in the Bering Sea and was hunted to extinction in the 1700s. The Steller's sea cow is related to the manatee and the dugong. Richard Ellis/Science Source

more centuries and many other extinction events for the concept to mature. Some noteworthy extinctions in this era are that of the Steller's sea cow in the mid-1700s, the African bluebuck around 1800, the Mauritius blue pigeon in the early 1800s, the great auk in the mid-1800s, and the Atlas bear, which was hunted out of the Atlas Mountains of Morocco in the late 1800s. Two particularly drastic and important cases of extinction and near extinction, both of which occurred in the United States in the 1800s, are revealing as to the scale of humanity's potential for impacting the environment. The passenger pigeon (*Extopistes migratorius*) and the American bison (*Bison bison*) were two of the most abundant animals on the North American continent until widespread hunting caused their populations to decline rapidly during the Industrial Revolution. These two case studies proved instrumental in the establishment of a more concrete moral and legislative foundation for conservation, as the implications for these species' collapses could not be clearer: If unrestrained, humans have the potential to devastate even the most abundant of species in mere decades.

The passenger pigeon

Ranging throughout eastern North America, the passenger pigeon was one of the most numerous bird species on Earth just two centuries ago. In the 1800s, the passenger pigeon was commercialized as a food source, and hunting was practiced on a massive scale; pigeons were hunted throughout the Midwest and shipped by railroad to eastern cities. The population declined slowly but steadily from about 1800 to 1870, before experiencing a catastrophic collapse between 1870 and 1890.

There were some attempts at curbing the rate of hunting before the bird was driven to extinction, but none of them was successful. In 1857 a bill was brought before the Ohio state legislature seeking protection for the passenger pigeon, but a committee of senators filed a report stating that "the passenger pigeon needs no protection. Wonderfully prolific,

Extinction

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Shooting passenger pigeons, which are now extinct, for sport in Louisiana c. 1870s. © North Wind Picture Archives/Alamy.

having the vast forests of the North as its breeding grounds, traveling hundreds of miles in search of food, it is here today and elsewhere tomorrow, and no ordinary destruction can lessen them, or be missed from the myriads that are yearly produced” (Hornaday 1913, 1). Other measures in Michigan and Pennsylvania sought to stop hunting and prohibit netting pigeons near nesting areas, but these were weakly enforced and proved too little, too late. The species was highly gregarious and apparently needed large flocks to court and breed. As their numbers diminished, their biology further inhibited their reproduction. The species entered an extinction vortex from which it could not return. Attempts at captive breeding failed, and the last known individual died in the Cincinnati Zoo in 1914.

The precipitous decline of the passenger pigeon, culminating in its extinction, was not in total vain, however, in that it proved to be one of the foremost examples that aroused public awareness of the potential impacts of human activities on species and raised interest in the need for conservation legislation. One other contemporary case equals the potency of this episode in terms of influence on the modern conservation movement—that of the American bison.

The American bison

The American bison, currently the largest native land mammal on the North American continent, once roamed the grasslands from northern Mexico to northern Canada in enormous herds. In the nineteenth century, hunting of the bison was rampant and actively endorsed by the US federal government for a variety of reasons, including reducing pasture competition for domestic livestock and weakening the populations of Native Americans that depended on bison for food and clothing. The railroad industry also worked to cull bison herds that threatened the safety of their new railways. The main cause of decline, however, was commercial hunting; bison hide was used for clothes, rugs, and industrial machine belts. By the mid-1880s the bison was dangerously close to extinction, with just a few hundred individuals left.

As the bison came perilously close to extinction and plans to save the species were discussed, the US government declined to play any significant role in the protection or recovery of the species. In 1874 President Ulysses S. Grant vetoed a bill that would have protected the remaining bison.

Endangered species

Extinction



Bison in snow at side of Yellowstone River © REBimages/Alamy.

In 1875 General Philip Sheridan of the US Army pleaded with the US Congress to allow the slaughter of the remaining bison to aid in the control of Native Americans (Bergman 2004).

The recovery of the bison was in fact a private endeavor, with ranchers purchasing bison to protect and breed, likely with some foresight into the potential to profit from the species. These small, private measures eventually led to the recovery of the bison, albeit in a limited fashion. As of 2012 there were an estimated 500,000 bison in captive commercial populations, but only about 30,000 individuals in wild herds, and only about 15,000 of these are deemed free roaming and truly wild. The only continuously wild herd of bison in the United States resides within Yellowstone National Park and numbers between 3,000 and 3,500 individuals (Bergman 2004).

Both the drastic decline of a once superabundant and emblematic large mammal species and the inability and disinterest of the US government in protecting the species brought alarm to various groups of Americans. Along with that of the passenger pigeon, the story of the American bison played a key role in instigating the natural resource management initiatives of the Progressive Era.

Early conservation legislation in the United States

Early American environmental philosophy tended toward a so-called myth of abundance. Experience soon showed, however, that wildlife in North America, while abundant, was not infinite. For example, the Massachusetts Bay Colony adopted a closed season on deer by 1693, and several other colonies soon followed suit (Goble 2006). During the Industrial Revolution, human capacity for development and consumption of resources increased greatly. These times were characterized by the idea that nature was a resource to be harvested in order to convert natural capital into private wealth.

In the 1890s the Progressive Era in US politics took shape, with the ideals of reducing corruption, promoting women's suffrage, and increasing efficiency in all sectors of the government, economy, and society. Progressives strongly supported the use of the scientific method in many areas. While not primarily a conservation movement, many of the ideals of the Progressive movement were applied to the environmental issues of the time. Considering the examples of the passenger pigeon and American bison, progressives believed that proper management of natural resources could allow for a more sustainable yield and therefore a more

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efficient and sustainable economy. Theodore Roosevelt, who served as president of the United States from 1901 to 1909, was one of the key proponents of this mode of thought, along with Gifford Pinchot, Roosevelt's appointee to head the newly established U.S. Forest Service. In describing the role of this new agency, which was formed in 1905, Pinchot summarized the mindset of the movement this way: "In the administration of the forest reserves . . . all land is to be devoted to its most productive use for the permanent good of the whole people, and not for the temporary benefit of individuals or companies" (Goble 2006, 9). Progressivism was an important step in the modern conservation movement, having established an ideology of utilitarian conservation in the United States that lasted until the 1960s. Many early attempts of the federal government to protect natural resources occurred in this era and are worth considering in some detail.

The Lacey Act of 1900, passed under the presidency of William McKinley (when Roosevelt was vice president), is regarded as the first federal law in the United States directed at the preservation of wildlife. In an attempt to address the overhunting of game animals, the law prohibited the transportation of illegally harvested game across state lines and also addressed the introduction of nonnative species to ecosystems. The act's primary focus was to preserve the populations of game animals through the regulation of interstate commerce, although it proved largely ineffective because it did not regulate hunting that occurred within states. In the early twenty-first century, the law is still used to discourage the importation and spread of invasive species.

As the Lacey Act proved largely ineffective at preventing the continued decline of migratory game birds, conservationists continued to lobby for more effective legislation. The Weeks-McLean Act, passed in 1913, asserted that the federal government had the authority to regulate the hunting of migratory birds directly (rather than simply in relation to interstate commerce). Nonetheless, the act was immediately challenged, and the Supreme Court ruled it was unconstitutional, as the regulation of hunting was deemed to be the role



A juvenile whooping crane in migration. Courtesy of operationmigration.org.

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of the states. In response to this ruling on the Weeks-McLean Act, Congress shifted tactics and pursued an international treaty for the protection of migratory birds with Great Britain—the Convention between the United States and Great Britain (for Canada) for the Protection of Migratory Birds of 1916. In order to implement this convention within the United States, Congress passed legislation providing authority to the federal government through the Migratory Bird Treaty Act of 1918. This act was also challenged in courts, much like the Weeks-McLean Act, but the climate of the US Supreme Court had changed, and this time the court ruled that "it is not sufficient to rely upon the States. The reliance is vain" (Goble 2006, 10). This important ruling opened the door for federal oversight and management of species.

Well after the dramatic declines of the passenger pigeon and American bison in the 1800s, the whooping crane (*Grus americana*) rekindled the urgency for conservation measures in conservation-minded Americans in the 1930s. The case of the whooping crane rose to notoriety when the population dropped below twenty individuals in the 1930s as a result of habitat destruction and overhunting. As a charismatic and elegant species, it became an important symbol of the conservation movement. In 1937 the Bureau of Biological Survey (a forerunner of the Fish and Wildlife Service) acquired the property for and established the Aransas National Wildlife Refuge in Texas to protect the wintering grounds of the whooping crane. As of 2012, the whooping crane survived as a result of an intense conservation program, with a total population of just a few hundred. Although the species continued to struggle for survival, it remained an important symbol of the conservation movement in the United States and of the difficulties in restoring a critically endangered species.

In 1940 Congress passed the Bald Eagle Protection Act, which sought to save a national icon of the United States from impending extinction. This law increased the federal government's powers to regulate harm to or killing of bald eagles anywhere in the nation and advanced the notion of the federal government's role in protecting endangered species. Also in 1940, the United States signed the first international convention on conservation since the 1916 treaty with Great Britain. The Convention on Nature Protection and Wild Life Preservation in the Western Hemisphere committed the United States, in bold language, to "protect and reserve in their natural habitat representatives of all species and genera . . . in sufficient numbers and over areas extensive enough to assure them from becoming extinct through any agency within man's control" (OAS 2012, 1).

Although the developments of the Progressive Era made significant improvements in the preservation of migratory birds and the protection of the bald eagle, these developments made for little improvement in the protection of most other biodiversity. While conservation philosophy greatly developed during this time, the actual legislation lacked significant tools to effectively preserve species. The 1960s brought about a new era in endangered species conservation that started with a burst of pro-conservation legislation.

The early modern era

The first attempt at a comprehensive federal endangered species act was the Endangered Species Preservation Act of 1966 (ESPA), which focused on the preservation of wildlife habitat in order to conserve native fish and wildlife threatened with extinction. Although the wording of the ESPA called for dramatic efforts to conserve species, the act had relatively few legislative tools and little funding, making it weak in its application. The ESPA did call for a formal listing of endangered species, and seventy-eight species were listed in 1968—likely the crowning achievement of the act.

In 1969 Congress attempted to remedy some of the weaknesses of the ESPA by placing more emphasis on the direct *take* of species and recognizing the international component of endangered species conservation. The modified act, renamed the Endangered Species Conservation Act (ESCA), sought to regulate interstate and international trade in endangered species and was backed by stiff civil and criminal penalties for noncompliance. The ESCA also called for the secretaries of the interior and state to convene an international conference on endangered species. The conference was eventually held in Washington, DC, in 1973 and succeeded in passing the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), a treaty that established an international system for the regulation of imports and exports of endangered species. As of 2012, CITES remained one of the most important international tools for the regulation of trade and the conservation of endangered species.

The ESPA and ESCA set an ideological framework for endangered species conservation legislation in the United States, but they lacked tools and a comprehensive plan for how to achieve the goals they outlined. The conservation movement was in full swing in the United States in the early 1970s, and the time was ripe for more comprehensive legislation. In 1973, the same year that the important CITES convention was established, the US Congress passed what has been regarded as the most important and comprehensive biodiversity conservation legislation the nation or world had seen to that date: the Endangered Species Act.

The Endangered Species Act of 1973

President Richard Nixon signed the Endangered Species Act (ESA) into law on December 28, 1973. It was one of the least controversial bills of 1973 to go through Congress, with versions being passed by the Senate by a vote of 92–0 and the House of Representatives by a vote of 355–4. At the time there was widespread popular concern for the decline of species and broad political consensus that the federal government needed better legislative tools to protect the nation's biological heritage. In reflection of this consensus, the ESA was shaped into what was widely regarded as the most authoritative, stringent, and comprehensive legislation dealing with endangered species conservation the world had ever seen.

The justification for the enactment of the law is based on three main findings:

1. Various species of fish, wildlife, and plants in the United States have been rendered extinct as a consequence of economic growth and development not tempered by adequate concern and conservation.
2. Other species of fish, wildlife, and plants have become so depleted in numbers that they are in danger of, or threatened with, extinction.
3. These species of fish, wildlife, and plants are of aesthetic, ecological, educational, historical, recreational, and scientific value to the nation and its people (Kubasek and Silverman 2005).

An important component of the act was the simple defining of the terms *endangered*, *threatened*, and *take*. In Section 3 of the ESA, these terms are defined as follows:

- “The term ‘endangered species’ means any species which is in danger of extinction throughout all or a significant portion of its range other than a species of the Class Insecta determined by the Secretary to constitute a pest whose protection under the provisions of this Act would present an overwhelming and overriding risk to man.”
- “The term ‘threatened species’ means any species that is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.”
- “The term ‘take’ means to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct” (NOAA 2012).

In its original phrasing, the ESA was clear about the importance of preserving biodiversity and specific about how to address the issue. It authorized the listing of “threatened” and “endangered” species, required federal agencies to ensure that their actions did not jeopardize a listed species, prohibited the unauthorized “take” of endangered species by any person, provided the federal government with the authority to acquire land for the conservation of listed species, and imposed civil and criminal penalties for infractions of the act (Scott et al. 2005a). The ESA states that a number of factors can contribute to a species’ threatened or endangered status, including the “present or threatened destruction, modification or curtailment of its habitat or range; overutilization for commercial, recreation, scientific, or educational purposes; disease or predation; the inadequacy of existing statutory mechanisms; or other natural or manmade factors affecting its continued existence” (Kubasek and Silverman 2005, 389).

The philosophy behind how the act would work is as follows: if a species is deemed endangered or threatened, it would be listed and critical habitat for the species would be determined. The USFWS, for terrestrial organisms, or the National Oceanic and Atmospheric Administration (NOAA), for marine and anadromous (species that use both marine and river systems) organisms, are then responsible for constructing a recovery plan for the species based on the best available science and determining how best to remove or mitigate the threats to the species in order for its populations to recover.

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During the recovery process, the species would receive full protection from harm from any agency or person, with civil and criminal penalties at the disposal of the USFWS or NOAA for enforcement (Scott et al. 2005a).

The act was rigid in its original design. The definition of *take*—the key term used in the act to define harming an endangered species—was comprehensive and allowed for little misunderstanding or loopholes. In one of the important early US Supreme Court cases testing the rigidity of the ESA, *Tennessee Valley Authority v. Hill* (1978), the Court decided that the law would “admit to no exception” for harm caused to an endangered species, in this case the snail darter, a small fish (Scott et al. 2005a). But in response to this Supreme Court decision, and as a result of changing political pressures, Congress began a long process of modifications to the original act, in order to reduce its rigidity and to seek a balance between endangered species conservation and human economic and private property interests.

Amendments and adjustments to the ESA

Below are summarized the most important amendments to the ESA.

1978

In 1978, in response to *Tennessee Valley Authority v. Hill*, Congress made significant amendments to the ESA. These amendments focused on the procedures necessary for listing a species as threatened or endangered, making the process significantly more complicated. In the listing process, the USFWS was now required to hold local hearings and include a designation of critical habitat before deciding whether to list a species. While the process became much more complicated, Congress also placed a two-year time limit on the process: Those listing decisions that were not completed within two years were to be withdrawn from consideration. The effects of these seemingly subtle changes in the listing process were profound: Fewer than 5 percent of the more than 2,000 species that were proposed for listing in 1978 were finalized, and on December 10, 1979, the USFWS withdrew listing proposals for 1,876 species (Scott et al. 2005a). By modifying the listing procedures, Congress changed what was originally simple and straightforward legislation into a significantly more complex and loophole-prone law.

1982

The next round of significant modifications to the ESA came in 1982, when Congress responded to an executive order by President Ronald Reagan that mandated the listings be economically justified. Congress rebuked this executive order by specifying that listing determinations were to be based on the best scientific data and not based on economic considerations. In this same round of amendments, however, Congress weakened the strict take guidelines outlined in the original version of the act, allowing for incidental takes of endangered species. Incidental take permits were established, which greatly reduced the stringency of the original legislation, permitting both federal agencies and individuals to take an endangered species so long as it would not

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“appreciably reduce the likelihood of survival and recovery of the species in the wild” (Scott et al. 2005a, 10). This amendment proved particularly important in the mid-1990s, when the execution of the ESA was significantly modified under the administration of President Bill Clinton to reduce conflicts with private property holders and in an attempt to increase the effectiveness of habitat conservation on private land.

1988

Amendments in 1988 focused on three themes: monitoring of recovered species, increasing the accountability of the government during the recovery process, and enhancing the protection of plant species. Specifically, the amendments required that a recovered species be monitored for five years and allowed it to be fast-tracked to relisting if the species is deemed threatened or endangered again during this period. In addition, species recovery plans were required to undergo a public notice and comment period, and federal agencies were required to consider these comments; biennial reports to Congress were required on the development and implementation of recovery plans and on the status of all species with recovery plans; federal and state governments were required to report all expenditures associated with endangered species recovery; and the protection of endangered plants was increased by including a prohibition on the malicious destruction of federal lands.

Executive branch actions in the 1990s

Arguably the most important modifications to the ESA came in the mid-1990s. Since its inception, a major point of contention under the ESA was the definition of *harm*. In the 1990s Bruce Babbitt, the US secretary of the interior, interpreted harm to mean “an act which actually kills or injures wildlife. Such [an] act may include significant habitat modification or degradation where it actually kills or injures wildlife by significantly impairing essential behavior patterns, including breeding, feeding, or sheltering” (Kubasek and Silverman 2005, 390). This broad definition of harm was challenged in court in the early 1990s, and after mixed rulings in lower courts, the definition was finally upheld by the US Supreme Court in 1995. The upholding of this broad definition significantly restricted the actions of landholders with endangered species or their habitat on the landholders’ private property. Although this decision was deemed an important victory for environmentalists, it was a contentious decision that, some believed, motivated property rights advocates against the ESA and brought a significant backlash to the legislation.

In response to the public backlash to this Supreme Court decision, Babbitt attempted to make administrative reforms to the act that would reduce the conflict between private property holders and endangered species conservation. He advocated strategies that were incentive based rather than penalty based in regard to endangered species conservation, and he helped expand the use of incidental take permits. Such permits had been authorized by the 1982 amendments to the act and included habitat conservation plans, candidate conservation agreements, and safe harbor agreements. A habitat modification plan is a mitigation plan for activities

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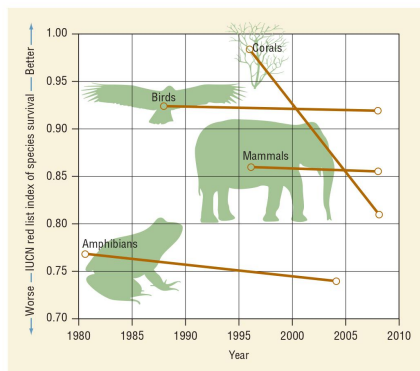


Figure 1. Red List Indexes (RLI) for reef-forming corals, birds, mammals, and amphibians. Coral species are moving towards increased extinction risk most rapidly, while amphibians are, on average, the most threatened group. An RLI value of 1.0 equates to all species qualifying as Least Concern (i.e., not expected to become Extinct in the near future). An RLI value of 0 equates to all species having gone Extinct. A constant RLI value over time indicates that the overall extinction risk for the group is constant. If the rate of biodiversity loss were reducing, the RLI would show an upward trend. Reproduced by permission of Gale, a part of Cengage Learning.

that involve the “take” of a listed species. When such a plan is authorized, the take of the species is authorized with agreed-on mitigation requirements to redress the harm caused. A candidate conservation agreement is a voluntary agreement between a landowner and the USFWS in which the landowner agrees to specified actions to conserve a species that is a candidate for listing under the ESA, with assurances that the federal government will not impose stricter guidelines on the landowner than those agreed on at the time. A safe harbor agreement can be issued by the USFWS when it is deemed that an action by a landowner “will provide a net conservation benefit to the affected listed species” (Scott et al. 2005b, 28). This is a method by which the USFWS can assure landowners doing a good deed on behalf of a listed species that they will not be penalized.

In general, these permits allowed for individuals and organizations to voluntarily agree to certain guidelines, and in return the federal government would assure them that no new restrictions would be placed on the use of their private land. The response to these modifications was mixed and quite heated at times. Some argued that these agreements were friendly toward the interests of private property rights advocates and developers and that they reduced the stringency and effectiveness of the ESA. Others argued that Babbitt’s incentive-based approach proved more effective at mitigating habitat destruction and reduced the contention between conservationists and private property rights advocates, helping establish a results-driven middle ground.

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Post-2000

There were some relatively minor amendments to the ESA between 2000 and 2012, but these were generally considered to pose only minor changes to the effectiveness or implementation of the law. The most important of these amendments came in 2004, when the US Department of Defense was exempted from critical habitat designations under the ESA under certain criteria.

Critical review of the ESA

Decades after its being signed into law, the ESA continued to be a cornerstone of US biodiversity policy and was among the nation’s most important environmental laws. As of 2012, however, there was vigorous debate regarding the efficacy of this legislation in protecting and restoring populations of endangered species. This section provides a review of the successes and criticisms of the act prior to 2013.

The numbers

When the Endangered Species Act was enacted in 1973, there were 392 species listed as endangered and threatened, composed of only vertebrate animal species (Scott et al. 2005b). As of January 2013, there were 1,434 domestic species on the list, including 621 animals and 816 plants, and an additional 615 foreign species (USFWS 2013b). The diversity of listed species has increased greatly over time, with the list beginning with a focus on vertebrate animals and then expanding to include a diverse array of wildlife, including plants and invertebrates. There are still biases evident in what is listed, however, including a notable underrepresentation of marine species (Armsworth et al. 2005).

As of February 2012, 36 US and foreign species or distinct populations of species had been removed from the USFWS endangered species list as a result of causes other than “original data error” since the inception of the law. Of these, 26 had been deemed “recovered,” and the remaining 10 species had gone extinct (Congressional Research Service 2012).

Criticisms of the ESA

There is a tremendous amount of scientific literature analyzing the effectiveness of the ESA, with a broad range of interpretations of its successes and downfalls. The primary criticisms of the act include the following:

1. it is underfunded;
2. it is reactionary rather than preventative;
3. it focuses on individual species rather than ecosystem health;
4. it is ineffective and controversial when addressing conservation on private property; and
5. it is impotent to address the magnitude of the conservation challenges of today.

In regard to funding, Joe Kerkvliet and Christian Langpap, in a 2007 study, found that increased spending on a species

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reduces the probability that the species will be declining or go extinct. Further, these researchers found that ESA-related spending is more effective in preventing declines than in promoting recovery: “Even though funds spent on threatened and endangered species may in general not lead to full recovery (and delisting), they seem to prevent further decline and eventual extinction” (508). One possible reading of this research is that attention (and funding) should be focused on declining species sooner, so as to invest in prevention and avoid the difficulties that endangered and threatened species face to recovery. Other researchers (e.g., Male and Bean 2005) have similarly found that spending is correlated with improved status.

When a species is imminently close to extinction, and therefore qualifies for listing under the ESA, it faces a number of biological challenges that inhibit recovery. In a 2005 study, Martin F. J. Taylor and colleagues found that species listed as threatened are more prone to have an improving status than species listed as endangered. They argued that the prompt listing of species, before their numbers are critically low or their habitat is extensively impaired, could significantly enhance the efficacy of the ESA. Nonetheless, current trends in listing tend to favor waiting until a species qualifies for endangered status. This was evident from the numbers for January 2013, when 1,109 domestic species were listed as endangered and 319 domestic species were listed as threatened (USFWS 2013b). Furthermore, Daniel J. McGarvey, in a 2007 article, argued that the current listing of endangered species incorporates an important error in thinking—one of being overly cautious in determining how and when to list species. When dealing with the listing of endangered species, he argued, it is much more harmful not to list a species that is indeed endangered than it would be to list a species that is not: “uncertainty should not constrain efforts to protect imperiled species . . . particularly when the threat of irreversible damage exists” (69).

The focus of the ESA on individual species rather than overall ecosystem health has also been a source of criticism. Some have argued that, in focusing on individual species, the act is inherently nearsighted and that a much more effective and efficient means of promoting conservation would be to focus on ecosystem health and habitat conservation. In a 2005 contribution, J. Michael Scott and colleagues stated that “the ESA is an at-risk *species* act—it is not a comprehensive *biodiversity preservation* act” (2005a, 4). For a 2001 study, Amy Whritenour Ando conducted economic analyses on the efficacy of endangered species programs, and she concluded that “there are sizable beneficial spillovers from the protection of one species in a county to the welfare of its neighbors. This suggests that a move toward an ecosystem or at least regional approach to species protection may make sense” (331).

The most contentious aspect of the ESA has been the regulation of privately owned endangered species habitat. Private property rights activists have argued that the ESA places an unjust burden on landowners to conserve endangered species. The majority of endangered species rely, at least in part, on private property for habitat. Langpap, in a 2006 article, pointed out that “more than half of the listed endangered

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species have at least 80% of their habitat on private land” (558–559). In order to reduce the conflict between conservationists and landholders, the USFWS promoted the use of habitat conservation plans (HCPs), which allow for some loss of endangered species habitat in exchange for long-term plans to minimize and mitigate the loss. These plans have been strongly criticized by some environmentalists who have argued that they undermine ESA take standards and contribute to the deterioration of endangered species habitat. Others have argued that compromises and assurances between the USFWS and private landholders have helped decrease preemptive endangered species habitat destruction and have fostered increased preservation of habitat.

As part of a 2007 study, Paul J. Ferraro and colleagues found evidence that there are surprising negative incentives for landowners to preemptively destroy habitat on their private property that may qualify as endangered species habitat. They found that, on average, the placement of a species on the endangered species list is actually detrimental to the status of a species if it is not combined with substantial government funds. “Shoot, shovel, and shut up,” a tendency for landowners to preemptively harm species and habitat on their private property to avoid future regulation of their land uses, has been widely documented. Furthermore, in a 2012 study, Langpap and Kerkvliet found that, on average, HCPs have had a positive effect on species recovery, citing evidence that, from 1990 to 2004, species with HCPs are more likely to show improvement in recovery status and less likely to be declining than species without an HCP. While HCPs may not be a perfect solution to the conservation of endangered species on private property, they may reduce conflict and thus have a net positive effect on the efficiency and effectiveness of the act.

The magnitude of the conservation challenge in the twenty-first century is truly awesome and will test the act over the coming decades (Scott et al. 2005a). As of 2012, more comprehensive legislation was needed to address such complex issues as increased habitat fragmentation, the spread of invasive species, human population growth, and global warming, among other factors, in order to successfully prevent extinctions and promote species recovery. In their 2005 contribution, Scott and his colleagues contended that

the ESA is a tool of last resort that can slow but not prevent the accelerating loss of biodiversity from the American landscape. Simply put, it comes into play too late. To prevent species from becoming endangered and thereby conserve our nation’s biological infrastructure, we must look beyond the ESA and craft ways to accommodate more native species in areas where we live, work, and recreate. (15)

Successes of the ESA

The ESA came under fire for not succeeding in recovering many species. In response, many argued that endangered species conservation is fighting against great odds and that recovery might not be the best metric for success, citing that the amount of time that the act has been in operation is relatively short (decades) compared to the time that species have been declining (centuries); that the recovery of some

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species may be near impossible as they are too close to the brink of extinction and are inhibited by demographic, genetic, and habitat limitations; and that the conservation and restoration of species is increasingly difficult in a world with a growing human population, increasing habitat destruction and spread of invasive species, and accelerating climate change. Despite these overwhelming difficulties, the ESA does have some positive results to show.

Writing in 2001, Gregory D. Hayward and colleagues argued that the “mismatch between the temporal scales of the extinction process and the implementation of the ESA” limits analysts’ ability to judge the ESA’s success given that, at the time their contribution was published, less than three decades had elapsed since the act’s passage (9). One alternative measure of the effectiveness of the ESA may be the capacity of the act to prevent the extinction of declining species—a criterion by which the act can be judged to have largely been successful. In a 1999 study, Mark W. Schwartz roughly calculated that ESA protection had prevented as many as 187 extinctions, by regulating takes, preserving habitat, and developing recovery plans.

In their 2005 study, Taylor and his colleagues argued that the ESA is effective legislation, based on their findings that (1) the longer a species is listed, the more likely it is to be improving; (2) species with critical habitat designation for two or more years are more likely to be improving; and (3) species with dedicated recovery plans for two or more years are more likely to be improving. They argued that the benefits of listing include recovery plans, protection from unauthorized takes, protection of critical habitat, increased scientific research, captive breeding, public education, and habitat restoration and acquisition. These findings suggest that these conservation measures are effective and that they act cumulatively over time. In order to improve the efficacy of the act, Taylor and his colleagues advocated the early listing of species, as they found threatened species to be more prone to recovery than endangered species, and also argued for the protection of critical habitat and the creation of dedicated recovery plans.

Prospects for the future

As of 2013 there was wide agreement that the Endangered Species Act could be made more efficient and effective. A few of the most common and compelling suggestions were to increase oversight and regulation of takes, increase data collection on species, modify the listing process, and increase incentives for conservation on private property. All of these calls for improvements, however, require increased funding—the key to improving the act’s effectiveness.

In a 2006 article, Fidel Hernández and colleagues argued that many recovery plans are limited in their effectiveness because they suffer from a lack of scientific data. These researchers argued that the data that do exist need to be used more effectively in order to create better recovery plans and that the development of academic–agency partnerships could help improve the use of existing data and foster further research in areas in which significant data are lacking. Partnerships between regulatory agencies and academics

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could increase the effectiveness of conservation expenditures by focusing research on areas of concern.

The most hotly debated aspect of the ESA is the conservation of endangered species on private property. Robert Bonnie, in a 1999 article, argued that mitigation banking of endangered species habitat may be an important improvement to the act. This concept would allow for landowners to destroy habitat legally if they were to buy mitigation credits. This money would be used to incentivize the protection and restoration of habitat in other areas and could allow specialists to plan where best to protect and restore habitat to benefit the species in question. Bonnie contended that mitigation banking could also significantly reduce conflicts between endangered species and private property advocates. Stephen Polasky and Holly Doremus, writing in 1998, argued that the current design of the act, by placing a huge burden on the government to identify and conserve habitat, while providing compensation to landowners only in extreme cases, provides little incentive for cooperation and the preservation of habitat. They also stated that, in order to address this problem, increased compensation, in the form of tax credits, land swaps, or other noncash measures, could be provided to landowners who forego development and provide habitat for listed species. Similarly, Polasky and Doremus argued that conservation policy should *reward* landowners who discover that they have endangered species on their land, rather than punishing them with regulations and penalties. These authors contended that endangered species preservation needs to do a better job of preserving species and habitat on private property to be successful, and they argued that society as a whole should bear the costs of endangered species conservation, rather than individual property owners. In his 2006 study, Langpap also found that incentives, particularly compensation and assurances, can be effective at improving the conservation of endangered species on private property and also provided evidence that the traditional regulatory approach to conservation on private property has generated perverse incentives for landowners to discourage the presence of endangered species on their property.

The ESA has served to protect hundreds of species from extinction and has directly and indirectly contributed to the preservation of millions of acres of habitat for wildlife conservation. Simultaneously, the ESA has affected human activities, such as ranching, logging, recreation, and development. Despite many successes, the US federal government is not meeting its self-stated goals as outlined in the ESA to recover endangered species. Increased funding and, arguably, significant modifications to the legislation may be necessary for this to occur.

International conservation strategies

Treaties are the primary international governmental mechanisms for promoting biological conservation. A treaty is a voluntarily signed agreement by member parties that are dedicated to championing a certain cause. Once signed, a treaty may be legally binding. Arguably the two most important international treaties pertaining to biological conservation are the Convention on International Trade in

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Endangered Species of Wild Fauna and Flora (CITES) and the United Nations Convention on Biodiversity. In addition, it is worth considering the important role of the International Union for Conservation of Nature (IUCN) in bringing together governmental and nongovernmental organizations to develop conservation strategies, as well as its Red List of Threatened Species, which is the international standard for the status assessment of species.

CITES

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has been called “perhaps the most successful of all international treaties concerned with the conservation of wildlife” (Kubasek and Silverman 2005, 435). Annually, the international trade in wildlife is estimated to be worth billions of dollars and to include hundreds of millions of plants and animals. The value of some species and their by-products on the international market is extremely high, and the demand for them places an enormous incentive for their harvest and trade. Such harvesting can have dire consequences on wildlife populations and has caused many species to decline to the point at which they are approaching extinction. Other traded species continue to be common, but the regulation of their trade is necessary to prevent overharvesting and a resulting decline. The goal of CITES is to regulate this trade in order to protect threatened and endangered species, as well as to prevent the declines of more common species. In the early 2000s, CITES provides varying degrees of oversight and protection for over 30,000 species.

CITES has its origins in the Convention Relative to the Preservation of Fauna and Flora in Their Natural State, signed in London in 1933. This agreement was sought primarily for the protection of African game species that were being heavily hunted and exported at the time. There were several other regional attempts at controlling the trafficking of wildlife in the mid-twentieth century, but none was sufficiently comprehensive at regulating the global trade, until CITES was signed into law by twenty-one countries in March 1973 (CITES Secretariat 2012). The treaty was planned and drafted as the result of a resolution by the International Union for Conservation of Nature (IUCN) in a 1963 meeting. The final text was agreed on in a convention in Washington, D.C., attended by eighty countries in March 1973. On July 1, 1975, CITES became law after being ratified by ten member countries. Since its founding, CITES has been one of the international conservation agreements with the largest memberships—by 2013, 177 countries had become members (CITES Secretariat 2013).

All import and export of species on the CITES species list is to be authorized through a licensing system. Each country is responsible for creating a management authority, in charge of administering the licenses, and a scientific authority, to advise on the effects of trade on the status of species. Species fall into three categories of regulation: Appendix I, II, and III. Appendix I species are endangered, and trade in these species will be authorized in only the most extraordinary of circumstances. Appendix II species are considered to be vulnerable to extinction if freely traded, and thus trade is highly restricted. Appendix III species are protected within a country that has ratified CITES and that is seeking the cooperation of other nations in protecting

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the species. Enforcement of the treaty is left to signatory countries. In the United States, it is implemented through and augmented by the Endangered Species Act (CITES Secretariat 2013).

In 2000 the IUCN completed a comprehensive review of CITES and drew the following conclusions:

- Through its monitoring requirements, CITES has developed the most comprehensive database on international trade in species.
- CITES has been very effective at reducing the trade in some species. The IUCN cited wild cats, nonhuman primates, bears, marine turtles, reptiles (skins), and plants as examples of successes.
- CITES has failed to effectively manage the trade of other species. The IUCN cited the rhinoceros as an example of this.
- There has been little study of the status or trade of most of the species on the CITES species list, so it is difficult to conduct a thorough analysis of the effectiveness of the legislation.
- The treaty has continued to evolve with the times, proving flexible. Several “innovative measures” have been ratified in subsequent conventions since 1973. This flexibility seems to be one of the best traits of the legislation (IUCN 2000).

The IUCN further highlighted the limitations of CITES, pointing out that while the goal is to conserve wildlife, and that while some of the species listed under CITES have been declining, these declines in many cases fall outside the jurisdiction of the treaty, which is responsible solely for regulating international trade in species. There are, of course, many other factors that can contribute to the decline of species. In its review, the IUCN stated that the limited scope of CITES also makes it difficult to evaluate the effectiveness of the convention, as a number of factors that are not overseen by CITES may contribute to the decline of listed species.

In a 2009 article, Max Abensperg-Traun argued that CITES could be improved by promoting incentive-driven conservation, rather than its current regulation scheme. He noted that the use of and trade in wildlife in developing countries is often an imperative rather than a choice and argued that incentive structures that are developed on local levels are likely to be more effective measures of preserving species. Abensperg-Traun called for the promotion of trade in alternate species, while regulating others, in order to offset the economic hardships in developing countries. Other key issues with CITES include a lack of scientific research on most CITES-listed species and a lack of enforcement. Member countries are responsible for enforcement but often lack the resources and training to adequately identify, much less regulate, the trade of the 30,000-plus listed species.

The Convention on Biological Diversity

In recognition of the value of biodiversity and the pressing threats to its wellbeing, the United Nations Environment

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Programme in 1988 called for a convention on biodiversity to address related issues. At a 1992 conference held in Nairobi, Kenya, the text of the Convention on Biological Diversity (CBD) was agreed on, and it was opened for signing later that year at the United Nations Conference on Environment and Development held in Rio de Janeiro, Brazil (also known as the Earth Summit). The CBD was implemented in December 1993 after being signed by 168 parties. It established three main goals: the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits from the use of genetic resources (Secretariat of the Convention on Biological Diversity 2000).

The goals of the CBD are comprehensive and forward thinking, arguing for a new global consciousness and plan for the protection of biodiversity and the fair and equitable use of natural resources. Signatories to the convention agree to “conserve and sustainably use biodiversity” and are required to develop national biodiversity strategies and action plans in relation to sectors of the economy, including forestry, agriculture, fisheries, energy, transportation, and urban planning. By signing the convention, nations also commit to identify and monitor biodiversity in need of conservation, establish protected areas, restore degraded ecosystems, promote traditional and indigenous knowledge of the sustainable use of biodiversity, manage invasive species, control organisms modified by biotechnology, promote public participation and awareness, and report on their progress in these areas (Secretariat of the Convention on Biological Diversity 2000). The convention’s authority comes from the Conference of the Parties (COP), which consists of all ratifying governments. The COP reviews progress, identifies priorities, and establishes work plans.

The CBD has provided an important framework under which nations can establish goals, oversee progress, highlight directions for future research, and distribute funding to developing nations. This convention, however, lacks any enforcement mechanisms to certify that biodiversity will be protected. In some ways it parallels the conservation legislation in the United States leading up to the Endangered Species Act, particularly the Endangered Species Preservation Act of 1966, which had lofty rhetoric espousing the conservation of species but few legislative mechanisms to enforce these goals. Likewise, the CBD has established a framework and ethic for international biodiversity conservation that may set the stage for more formidable and binding legislation in the future.

IUCN

The International Union for Conservation of Nature (IUCN) is the world’s oldest and largest international network promoting environmental conservation. It has a democratic structure for determining policies and has a membership that includes more than 1,000 governmental and nongovernmental organizations worldwide, with a mission to “influence, encourage and assist societies throughout the world to conserve the integrity and diversity of nature and to ensure that any use of natural resources is equitable and ecologically sustainable” (IUCN 2013a). In practice, the IUCN supports scientific research, manages field projects, and brings governmental and

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nongovernmental organizations together to develop and implement conservation policy. Importantly, the IUCN publishes the Red List of Threatened Species, the world’s most comprehensive conservation status list for species. The stated goal of the Red List is to “provide information and analyses on the status, trends and threats to species in order to inform and catalyze action for biodiversity conservation” (IUCN 2013c). In 2012 the Red List included nearly 66,000 species assessments, almost four times as many as were included in 2000. Further, the list has expanded from the original focus on mammals and birds to include most other taxa (Godfrey et al. 2008).

The current global status of species

According to the most recent analysis of the Red List, conducted by Jean-Christophe Vie, Craig Hilton-Taylor, and Simon N. Stuart and colleagues, an estimated 1.8 million species have been described by science (Vié et al. 2009). Estimates of the actual number of species in existence vary widely—from 2 million to 100 million—but tend to converge around 8 million to 9 million species (Mora et al. 2011). However, a recent review estimates the number of species in the world as 5 ± 3 million (Costello et al., 2013). As of 2012, only 3.8 percent of the world’s described species have had their status assessed by the IUCN’s Red List. There are strong biases regarding which species have been assessed, favoring terrestrial vertebrates and plants in well-studied regions of the globe. Nevertheless, these assessments still provide an important window into the trends in species worldwide. In general, species that are restricted in their geography and dispersal ability are more vulnerable to extinction than the converse. For example, as a group, amphibians are more threatened than birds, while the range-restricted cycads are more threatened than the more cosmopolitan conifers.

In addition, this same report highlighted the general scientific consensus that climate change will play an increasingly important role in driving species extinctions (e.g., Sekercioglu

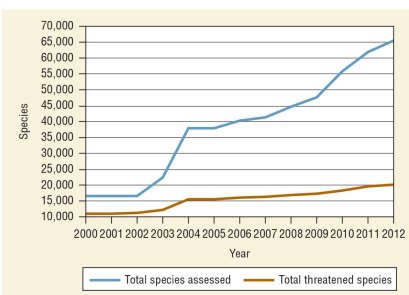


Figure 2. Assessed species versus threatened species. Reproduced by permission of Gale, a part of Cengage Learning.

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et al. 2012; Wormworth and Sekercioglu 2011). Particularly vulnerable are species that have specialized habitats, have narrow environmental tolerances, depend on interspecies interactions, or have limited dispersal ability. The report conducted more specific assessments of the susceptibility to climate change of three groups and found that 35 percent of birds are particularly susceptible, 52 percent of amphibians, and 71 percent of warm-water reef-building coral species.

As of 2008, there were 869 recorded extinctions, with an additional 290 species that were listed as “possibly extinct.” In addition, 3,246 species were listed as critically endangered; 4,770 as endangered; 8,912 as vulnerable; and 3,796 as near threatened. Also at that time, 5,570 species were listed as data deficient, while 17,675 species were determined to be of least concern. Of all the assessed species worldwide, 38 percent were threatened with extinction (listed as critically endangered, endangered, or vulnerable; Vic et al. 2008). These numbers are indicative of a world out of balance. Urgent and comprehensive conservation strategies are necessary to slow or reverse these disturbing trends.

The future is ours to write

The endangered species concept has a long history with origins dating back centuries, but it has developed greatly over the last several decades into a topic of utmost interest and concern in modern society. Different philosophies for why endangered species are important to conserve have been developed and expanded on, with arguments citing the ecosystem services provided by biodiversity, as well as the ethical and even religious responsibilities that humans may have to nature.

In 1973 the United States enacted the Endangered Species Act, which is regarded as the most comprehensive and stringent endangered species legislation the world has ever

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seen. While the act has succeeded in some instances, it has been criticized as being ineffective at fulfilling its goal of preventing extinctions and restoring populations of threatened and endangered species. The most important legislation internationally, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, has sought to regulate trade in threatened and endangered species, while the United Nations Convention on Biodiversity has encouraged biological conservation through the establishment of biological reserves, the promotion of cooperation and education, and the facilitation of the funding of projects in developing countries. International legislation has also had some important successes but is limited and nonbinding, relying on countries to join voluntarily and to self-enforce. With funding for regulation and conservation lacking, species have continued to decline both in the United States and internationally since the inception of these laws, proving that the existing strategies have been largely insufficient at protecting and restoring species worldwide.

In the early 2000s, endangered species conservation is likely more pressing and difficult than it has ever been. Species are increasingly threatened by the continued growth of human populations, the ongoing destruction of habitat, and the ominous threats posed by global warming. As mentioned above, 38 percent of all evaluated species have been deemed threatened with extinction. Yet, there is hope. The existing body of national and international legislation, scientists’ rapidly expanding knowledge of natural systems, and the growing concern for the environment among younger generations provide a framework from which to springboard into the next era of biological conservation—an era that humanity should feel compelled to define anew. While endangered species conservation is up against great odds, the ethical and economic importance of maintaining biodiversity merits great measures.

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APPENDIX B

AVIAN ECOLOGICAL FUNCTIONS AND ECOSYSTEM SERVICES IN THE TROPICS

Şekercioğlu, Ç.H. and E.R. Buechley. 2017. Avian Ecological Functions and Ecosystem Services in the Tropics. in *Why Birds Matter*. eds. Ç.H. Şekercioğlu, D.G. Wenny, C.J. Whelan, 321–340. Chicago: University of Chicago Press. Reprinted with permission from University of Chicago Press.

CHAPTER ELEVEN

Avian Ecological Functions and Ecosystem Services in the Tropics

Çağan H. Şekercioğlu and Evan R. Buechley

Birds contribute many important ecological functions through their roles as predators, pollinators, scavengers, seed dispersers, seed predators, and ecosystem engineers. Many of these ecosystem functions also translate to ecosystem services, which are defined as natural processes that benefit humans (Şekercioğlu 2010). Birds' abilities to fly and migrate enable them to respond to eruptive resources and to connect varying landscapes in ways that other organisms cannot. Further, the impressive diversity of birds (over 10,500 species) is indicative of their vast adaptive variety, which enables them to fill a wide diversity of niches. While there has long been interest in the relationship between birds and agricultural crops, dating from the 19th century in the United States, targeted research in this field largely lay dormant until the latter part of the 20th century (Whelan et al. 2008, 2015). To date, the vast majority of research on avian ecosystem services and agriculture has taken place in temperate climates, with relatively little research being done in the tropics. Nonetheless, over the last decade in particular, there has been a growing body of research in this regard, particularly in the Neotropics.

Although less than 1 percent of the world's bird species primarily prefer agricultural areas, nearly a third use such habitats occasionally (Şekercioğlu et al. 2007), often providing important ecosystem services such as pest control, pollination, seed dispersal, and nutrient deposition (Sodhi et al. 2011). Even though most bird species are found in the tropics, studies of

functional change in bird communities are disproportionately focused on European and North American ecosystems (Şekercioğlu 2006b). There is growing interest in avian functional diversity in tropical forests and agroecosystems, and especially in tree-dominated agroforestry systems, such as shade coffee and cacao plantations, which harbor higher bird diversity than do open agricultural systems with few or no trees (Thiollay 1995; Greenberg et al. 1997; Greenberg et al. 2000b; Wang and Young 2003; Perfecto et al. 2004; Waltert et al. 2005; Marsden et al. 2006; Clough et al. 2009; Tschardt et al. 2008; Van Bael et al. 2007; Kellermann et al. 2008). However, recent research has focused disproportionately on Neotropical coffee plantations (Komar 2006), and we need more studies on other types of tropical agroforest systems (Marsden et al. 2006; Round et al. 2006), particularly in Africa (Naidoo 2004; Waltert et al. 2005; Holbech 2009; Buechley et al. 2015) and on Pacific ocean islands (Marsden et al. 2006). There is a need for a global synthesis of these studies in order to understand how bird communities and the proportions of bird functional groups such as granivores, frugivores, insectivores, and nectarivores change from forests to agroforests to open agricultural systems. Not only is this important for a better understanding of the ecology of tropical bird communities and for improvement of tropical bird conservation, but also for estimating the changes in birds' ecosystem services (Wenny et al., 2011) and for calculating the economical contributions of these services to tropical farmers' incomes.

The objectives of this chapter are (1) to review the tropical avian ecology literature in order to quantify the changes in bird functional groups in tropical forests, agroforest, and agricultural areas, and (2) to improve our understanding of the changes in bird ecosystem services and ecological function in tropical agroforests and agricultural areas as a result of the declines or increases in predators, seed dispersers, pollinators, and other avian functional groups. We reviewed studies that compared tropical agroforestry and open agricultural ecosystems to native forests nearby. We used the combination of keywords “bird* AND tropic* AND forest* AND [agriculture OR agroforest]” in the Web of Knowledge database and in Google Scholar to generate a list of peer-reviewed research articles published between 1970 and 2015. Of these, we chose relevant articles that compared tropical forest birds to agroforest birds, open agricultural birds, or both. Under forests, we included natural primary or secondary forests and woodlands, and excluded plantations. Most tropical woodland species also spend time in forests, so they were included in the analyses.

Agroforests are defined as agricultural areas that have significant tree cover, such as cocoa, rubber, or shade coffee plantations.

Avian Community Structure

Tropical forest biodiversity is often highly specialized and reliant on little-disturbed forest (Turner and Corlett 1996). Nonetheless, agroforests are an important habitat for biodiversity conservation in the tropics, particularly when they are less intensively managed and have high canopy cover (Bhagwat et al. 2008). Although the variety of schemes used in the literature for guild classifications makes generalizations difficult (Komar 2006), some important patterns emerge. When agroforest systems are compared to primary forests, the species numbers of large frugivorous and insectivorous birds (especially terrestrial and understory species) are often lower (Tsharntke et al. 2008). In contrast, nectarivores, small to medium insectivores (especially migrants and canopy species), omnivores, and sometimes granivores and small frugivores do better or even thrive in agroforest systems (Petit et al. 1999; Vereá and Solozano 2005; Neuschulz et al. 2011; Ruiz-Guerra et al. 2012), frequently by tracking seasonal resources (Greenberg et al. 1997; Johnson and Sherry 2001; Carlo et al. 2003). However, changes in guild species numbers do not necessarily translate to changes in relative abundance (Vereá and Solozano 2005; Marsden et al. 2006), biomass, or function (Greenberg et al. 2000b; Perfecto et al. 2004), and more research is needed to quantify these important measures (Beehler et al. 1987; Komar 2006).

Neotropics

Tropical agroforestry systems often vary in their functional diversity patterns, but insectivores often have lower representation than in forests. In Paraguay, in *yerba mate* plantations shaded by forest trees located close to extensive forest, fruit and insect eaters, insectivores, and nectarivores were less abundant than in nearby forest, and two-thirds of carnivorous species were not found in plantations (Cockle et al. 2005). More than 60% of the birds captured in the understory of Venezuelan shaded cacao plantations were hummingbirds, whereas insectivores had reduced abundance and species richness (Vereá and Solozano 2005). Shade cacao plantations in southeast Brazil had fewer species of frugivores and understory insectivores, and more species of nectarivores and omnivores, than nearby forest

fragments (Faria et al. 2006). Landscape effects were not pronounced, although the proportional representation of frugivorous species was higher, and that of gleaning insectivores was lower, in the less forested landscape. Barlow et al. (2007) documented significantly more species in primary forest than in second-growth or *Eucalyptus* plantations in the Brazilian Amazon. Primary forest and *Eucalyptus* plantations had almost no species in common. Obligate ant-following and dead-leaf-gleaning insectivores were only recorded in primary forest, arboreal omnivores were most abundant in second growth, and there was a low relative abundance of external bark-searching and terrestrial gleaning insectivores in *Eucalyptus*. *Eucalyptus* also had a high relative abundance of nectarivores. In Ecuador, Canaday (1996) studied changes in the insectivorous bird community along a gradient of human impact, finding a significant reduction in the number of insectivorous birds in areas of greater human impact, including petroleum exploration and small-scale agriculture. In Mexican cacao plantations shaded by 60 species of planted native trees, but isolated from other extensive forest patches, forest specialists were scarce and resident insectivorous species were mostly missing, whereas small foliage-gleaning insectivores comprised most of the migrant birds (Greenberg et al. 2000a). However, omnivorous or frugivorous bird species were also few, again suggesting the importance of landscape composition. In Mexican shade coffee plantations, disturbance-sensitive bark insectivores, understory bark insectivores, and large canopy frugivores had fewer species than did native forest, whereas facultative and obligatory insectivores, omnivores, and midstory and understory/undergrowth granivores increased in shade coffee (Leyequien et al., 2010). On the other hand, Mexican tropical dry forests and tree orchards did not differ in their guild composition (Mac Gregor-Fors and Schondube 2011). In cacao farms in Panama, the diversity of birds and the diversity of canopy tree species were strongly positively correlated (Van Bael et al. 2007). In Costa Rica, one study documented higher species richness in forest edge than in coffee farms, active pasture, or fallow fields (Hughes et al. 2002), while another study found bat and bird assemblages in agroforestry systems to be as abundant and diverse as in forest; however, the species assemblages were highly modified and contained less forest specialists (Harvey and González Villalobos 2007). Another study in Costa Rica contrasting cacao plantations and forest patches documented higher avian density and diversity in cacao, but significantly fewer forest specialist species (Reitsma et al. 2001). In a long-term study (1960–99) of the effects of the conversion

of lowland tropical rainforest to agricultural habitat in Costa Rica, Sigel et al. (2006) documented insectivore declines while vegetarian and omnivorous species increased.

Afrotropics

In Ethiopia, shade coffee farms had more than double the species richness of nearby primary forest, while there was a much higher relative abundance of forest specialists, understory insectivores, and Afrotropical-resident understory insectivores in primary forest (Buechley et al. 2015). In these traditional, organic shade coffee plantations where coffee was grown in its native habitat under native forest trees, there were some results that contrasted with most global findings: (1) there was no difference in the relative abundance of insectivores between the two habitats, and (2) there was greater relative abundance of granivores in primary forest. In another study in Ethiopia, considerable overlap was found in species assemblages, higher abundances of open and shrubland bird species were documented at agricultural sites, and higher abundances of woodland and forest species were found in forest patches (Gove et al. 2008). In Kenya, bird communities were sampled in agricultural habitats surrounding a forest reserve to evaluate the habitat characteristics that influence bird diversity and abundance (Otieno et al. 2011). The results indicated that hedge volume was the most important factor in vegetation structure in agriculture, which correlated with bird species richness and insectivorous bird density. The bird density was also shown to increase with overall tree density. In another Kenyan study, bird communities were sampled at 20 sites along a habitat gradient from primary forest to intensive agriculture (Mulwa et al. 2012). The bird density and species richness was higher on average in agriculture than in forest habitat; but within forest and agriculture, density and richness increased with vegetation complexity. Importantly, the bird assemblages in forest and agriculture were distinct, with very few forest specialists occurring in agriculture. Insectivores declined in farmland, while carnivores and herbivores increased. Unusually, in Uganda there were no differences between forests and smallholder agricultural areas in the detection rates of insectivores versus noninsectivores, whereas larger, mostly frugivorous birds were more likely to be detected in the agricultural areas (Naidoo 2004). Newmark (1991) showed a decreasing richness of understory species with shrinking forest patch size in the Usambara Mountains of Tanzania. Insect gleaners, frugivores,

salliers, and seed eaters were less frequent in forest fragments than in a large forest control site. In Cameroon agroforestry systems with relatively high tree cover surrounded by primary forest, Waltert et al. (2005) observed reduced species richness compared to primary forest, and in some cases abundance of insectivorous species, especially those of the understory. Frugivores and omnivores did not differ, whereas nectarivores and granivores had higher richness in agroforests. In Ghana, Holbech (2009) found the trophic organization of the lower-story birds in luxuriant tree plantations to be similar to that found in native forest, though there were fewer ant-following birds in the plantations (69% of the numbers found in the forest). Cardamom (*Elettaria cardamomum*, *Amomum costatum* and *Amomum subulatum*) and coffee (*Coffea arabica* and *Coffea robusta*) plantations were better for forest birds than were cacao (*Theobroma cacao*) plantations. In the plantations, the presence of a canopy per se was more important than the number of species making up the canopy, and the choice of native versus exotic tree species was less important than the presence of a well developed and diverse secondary plant community, especially in the subcanopy layers (Holbech 2009). A similar finding was reported by Najera and Simonetti (2010) in a review of 167 case studies from 32 countries comparing birds in forests and in plantations. Sixty-eight percent of forest bird species were sensitive to “edge-effects” in Madagascar; the canopy insectivores were edge-sensitive, while the sallying insectivores preferred edges (Watson et al. 2004). In an unusual finding, frugivores declined at the forest edge in comparison to the forest interior. In a regional review of conversion of forest to agricultural and human-dominated landscapes in West Africa, Norris et al. (2010) showed a decline in insectivores and large-foliage gleaners in secondary forest as compared to primary forest. In cacao agroforests, ant followers, insectivores, and species with restricted distributions declined, while nectarivores increased; in annual crops the bird species richness was lower, and ant followers, insectivores, and foliage gleaners were replaced by granivores and nectarivores.

Indomalayan and Australasian Tropics

In traditional agroforests in tropical China, there were no consistent differences in bird guilds between economic forests, monsoon evergreen broadleaf forests, and montane rain forests (Wang and Young 2003); but this was not the case for other Asia-Pacific sites studied. Compared to

nearby primary forest, the fruit orchards of Thailand were dominated by smaller frugivores, nectarivores, and widespread generalists, whereas understory insectivores were poorly represented (Round et al. 2006). There was a 60% reduction in bird species richness in oil palm and rubber plantations in southern Thailand as compared to forest (Aratrakorn et al. 2006). Insectivores and frugivores were particularly susceptible to declines, while omnivores fared much better. There was little difference in bird community composition between the two plantation types. In Malaysian mixed agricultural habitats consisting of oil palms, rubber, and fruit trees, smaller primary forest frugivores and trunk-feeding insectivores tended to persist, whereas ground and understory birds were likely to disappear (Peh et al. 2005). Malaysian oil palm plantations, rubber tree plantations, and orchard gardens had only a third of the bird species found in the nearby primary forest, but the proportions of insectivores and frugivores did not differ between habitats (Peh et al. 2006). Schulze et al. (2004) showed a decline in bird species richness from forest ecosystems to agricultural ecosystems in Sulawesi, Indonesia, including a significant reduction in the number of insectivorous birds. They showed a positive relationship between the number of tree species and the number of endemic bird species, frugivores, and nectarivores. In another study in Sulawesi, bird species richness decreased from primary and secondary forest to cacao agroforestry (Waltert et al. 2004). The agroforests supported few frugivores and nectarivores when compared to primary and secondary forest. In Sulawesi cacao plantations, frugivores and nectarivores had lower species richness at increasing distances from the forest, while in granivores the opposite trend was found (Clough et al. 2009). Increasing the tree cover in these cacao plantations led to higher species richness in frugivores and insectivores. Bowman et al. (1990) studied bird community structure along a successional gradient of forest and slash-and-burn agriculture in Papua New Guinea. The primary forest supported more specialist feeders, including frugivores, nectarivores, and branch gleaners, while obligate granivores were restricted to open grassy habitats. In southern India, while the bird species richness varied very little across landscapes, there was significant variation in the composition of bird communities in different habitats (Sidhu et al. 2010). Tea and teak plantations were found to harbor fewer rainforest species, while coffee and cardamom plantations with more native shade trees supported more sensitive rainforest species. A study in Sumatra contrasted rubber plantations, rubber agroforest, and forest, finding that the avian species richness was similar between rubber

and agroforest, while lower in the plantations, and that the number of forest specialists was lower in agroforest and plantations than in forest (Beukema et al. 2007). In another Sumatran study, larger frugivores, larger insectivores of both canopy and understory, and terrestrial insectivores of the forest interior had mostly disappeared from the agroforests, while small frugivores, smaller foliage-gleaning insectivores, nectarivores, and edge species persisted (Thiollay 1995). Similarly, large frugivores, some insectivores, and ground foragers declined in the small-scale mixed agriculture-agroforestry systems of Papua New Guinea (Marsden et al. 2006). In a meta-analysis of studies from the region, Koh and Wilcove (2008) showed that oil palm plantations in southern peninsular Malaysia and Borneo harbor 77% fewer forest bird species than does primary forest. Worldwide, insectivorous birds are 40% less frequent in tree plantations, whereas the proportion of granivores is more than three times higher (Najera and Simonetti 2010). In a global analysis of 6,100 entirely tropical bird species, Şekercioğlu (2012) found that the species richness of large frugivorous and insectivorous birds (especially terrestrial and understory species) often declines in agroforests in comparison to primary forests. In contrast, nectarivores, small-to-medium insectivores (especially migrants and canopy species), omnivores, and sometimes granivores and small frugivores do better, frequently by tracking seasonal resources.

Avian Ecosystem Services

As demonstrated above, avian richness, abundance, and guild structure is often influenced by habitat modification in agricultural landscapes. Several studies show that arthropod abundance and plant herbivory increase when birds are artificially excluded from agricultural crops (Van Bael and Brawn 2005; Kellermann et al. 2008; Maas et al. 2015). However, it remains unclear how bird community structure impacts insect control, seed predation, seed dispersal, and other ecosystem services; further research is needed in this regard.

In Jamaica, coffee plants with birds artificially excluded had significantly higher coffee borer infestation, more borer broods, and greater berry damage than did control plants (Kellermann et al. 2008). Lower infestation on control plants correlated with higher total bird abundance, but not with specific avian insectivore abundance or vegetation complexity. Pest reduction by birds economically benefited coffee farmers in Jamaica by US\$310 per hectare (Johnson et al., 2010). Railsback and Johnson (2014) modeled the avian ecosystem services and habitat usage

in Jamaican coffee farms, and concluded that when considering both bird conservation and economic production, shade coffee is preferable to splitting the landscape into forest and sun coffee, because shade coffee supports more birds and benefits more from ecosystem services. Bird enclosure experiments in Panama revealed that birds decreased arthropod densities and leaf damage in the forest canopy during the dry seasons but not the wet ones, and that birds had no effect on the arthropod abundance in the forest understory (Van Bael and Brawn 2005). In Costa Rica, bird enclosures led to an increase in herbivorous arthropod abundance, which in turn led to an increase in leaf damage (Karp and Daily 2014). In a tropical forest restoration experiment in Costa Rica, the insect biomass was highest on tree branches where both birds and bats were excluded, and lowest where neither were excluded (Morrison and Lindell 2012). Interestingly, the predation rates on artificial Lepidoptera larvae in Mexico during the dry season were significantly higher in forest fragments than in continuous forest, potentially due to the less diverse yet more dominant avian insectivore community in forest fragments (Ruiz-Guerra et al. 2012). In a study of seed dispersal by birds in Costa Rica, bird abundance, not richness, best predicted the richness of bird-dispersed seeds (Pejchar et al. 2008). In Brazil, a study of seed dispersal by frugivorous birds showed that isolated trees attracted a greater and more distinct bird assemblage than did trees in forest fragments, and that the seeds of isolated trees were more likely to be dispersed to the largest variety of surrounding habitats (Pizo and dos Santos 2011). A few bird species were particularly important for the long-distance dispersal of seeds, making them valuable links connecting forest fragments. In Tanzania, when birds and bats were excluded from coffee shrubs with nets, there was a significant reduction of fruit set and fruit retention (Classen et al. 2014). Surprisingly, though, there was no difference in ecosystem services along a gradient of land-use intensity. In Kenya, frugivore richness and density declined with forest disturbance in three different rain forest study sites, thus suggesting a regional trend of forest disturbance leading to a decline of frugivores and their valuable seed dispersal services, particularly for large-seeded tree species and trees with small fruits (Kirika et al. 2008). In a study of three frugivore species in the Taita Hills of Kenya, differences in mobility and habitat use caused significant differences in seed dispersal (Lehouck et al. 2009). The most sedentary and forest-dependent species contributed to short-distance dispersal, often within the same forest patch, while the two more mobile species dispersed seeds further away from parent trees, and often into different forest patches or exotic plantations. This suggests that

seed dispersal by different species can be complementary, contributing to dispersal into a range of different habitats over varying distances. Retaining frugivore diversity may be integral to maintaining dispersal function. In Ghana, a study of dispersal of the large seeds of *Antiaris toxicaria*, an important timber species, concluded that mammals were responsible for 76.3% of seed dispersal, while birds were responsible for 23.7% (Kankam and Oduro 2009). The authors note, however, that dispersal by birds and fruit bats may be more effective because they are more mobile foragers. They conclude that a population reduction of seed dispersers can affect recruitment of tropical trees, and they suggest conservation of frugivores in order to promote the sustainable management of *A. toxicaria*.

In Borneo, bird exclusion significantly increased herbivory damage to oil palms—up to 28% foliage damage (Koh 2008). The author suggests that this may lead to a fruit yield loss of 9 to 26%. Oil palm is an important agricultural crop, suggesting that insectivorous birds provide important services to farmers in the form of insect control. In the Mariana Islands, a loss of bird diversity caused by the invasive brown treesnake *Boiga irregularis* has led to reduced recruitment in several Mariana Island tree species, many of which are dependent on birds for pollination and dispersal (Mortensen et al. 2008). In Hawaii, seed dispersal by native and introduced bird species was studied in dry forests (Chimera and Drake 2010). The authors found that although trees covered only 15.2% of the study area, 96.9% of the bird-dispersed seeds were deposited beneath them. The invasive bird *Zosterops japonicas* was the leading seed disperser, and of the bird-dispersed seeds, 75% were of the invasive tree *Bocconia frutescens*, while the invasive shrub *Lantana camara* accounted for an additional 17%. Exotic bird species were found to rarely disperse the seeds of native tree species, and less than 8% of all bird-dispersed seeds were from native trees. This suggests that avian seed dispersal can operate both as a service and a disservice, depending on which species of seeds the birds are dispersing, particularly when the birds in question are exotic species. This study concludes that current dispersal patterns are likely to contribute to the replacement of native flora by exotic plants in Hawaiian dry forests.

Discussion

The results of the findings of field studies in Neotropical (Leyequien et al., 2010), Afrotropical (Waltert et al. 2005), Indomalayan (Peh et al. 2006),

and Australasian (Marsden et al. 2006) regions suggest that the replacement of forests with agricultural areas results in a shift towards less specialized bird communities comprising more widespread and relatively common species, and with altered proportions of functional groups (Şekercioğlu 2012). Insectivores and other invertebrate predators often make up a smaller proportion of bird communities outside forests, whereas seed-dispersing frugivores and pollinating nectarivores are higher in agroforests, especially as compared to open agricultural areas that can experience substantial increases in avian seed predators in comparison to forests and agroforests. Given that there are considerable differences in functional distribution, specialization, global range, population size, mobility, and conservation status between forest, agroforest, and agricultural bird communities, there is an urgent need for detailed field studies that compare bird community ecology and avian function in these habitats.

Agroforest birds are likely to be the primary seed dispersers in agricultural areas, a pattern also observed in the field (e.g., Pizo 2004). Integrating agroforests with open agricultural areas may result in a spillover of nectarivores and partially make up for the decline in avian pollinators among open agricultural species. The high primary productivity of agroforestry in the tropics is likely to attract more fruit- and nectar-eating birds than birds of other groups. Since trophic cascades are more likely in more productive ecosystems (Van Bael et al. 2003), reductions in insectivorous bird species in simplified agricultural systems may lead to increases in insect outbreaks (Mellink 1991). The use of pesticides to control insect pests in agricultural areas may offer a poor prey base for insectivorous birds. This is counterproductive for agriculture, as insectivorous birds can be important by removing and controlling insect pests (Greenberg et al. 2000b; Perfecto et al. 2004; Johnson et al. 2010). The low richness and low numbers of insectivorous forest birds in agricultural areas may also be due to their poor dispersal abilities (Şekercioğlu et al. 2002).

Higher mobility and better dispersal capacity often improve the ability of birds to adapt to land-use change and can reduce the likelihood of extinction, as is indicated by the fact that long-distance migratory bird species are 2.6 times less likely to be threatened or near threatened with extinction than are sedentary species (Şekercioğlu 2007). Field studies on the intensification of coffee management on local bird species also indicate that resident sedentary birds are more sensitive than long-distance migrants to alteration of their habitat (Mas and Dietsch 2004). Even though resident birds decline in response to the conversion of native habitats

to coffee plantations, Wunderle (1999) found no effect of plantation size on migrant bird populations. Many migrants make extensive use of habitats with intermediate disturbance, such as shade coffee and other agroforests. Consequently, there may be some conservation trade-offs if the migrant birds reach higher numbers at lower levels of shade (tree cover), and some drop-off in numbers as tree cover increases to levels that benefit the residents more. Such potential conservation trade-offs in different groups needs more study.

Many published studies on agroforest avian communities have focused on Neotropical coffee (Komar 2006) and, to a lesser extent, cacao plantations. We need more research in other agro-ecosystems (particularly traditional mixed agroforests) and in different parts of the world. This is especially important since some studies in other regions and on different agroforest types have found no differences among avian guilds and have observed patterns contrary to the general trends revealed in this review and in global analyses (e.g., Buechley et al. 2015). The research on shade-grown coffee and cacao provides a sound foundation, but it can be improved by incorporating distinctive aspects of regional ecology with more targeted research. There is also a need for studies focused on raptors and seed eaters in agroforest systems, since these groups can be important pest and seed predators respectively, but remain understudied in agroforestry systems (Komar 2006). Furthermore, we know next to nothing about the impact on tropical forests and agroforests of the global declines in avian scavengers (Buechley and Şekercioğlu 2016a, 2016b).

Agro-ecosystems frequently comprise the matrix in which forest fragments, protected areas, and other native habitat remnants are embedded. Tropical agro-ecosystems often have substantial amounts of arboreal vegetation in the form of remnant trees (Fischer and Lindenmayer 2002), living fences (Harvey et al. 2005), riparian strips (Martin et al. 2006), and agroforestry plots (Schroth et al. 2004), all of which often have conservation values disproportionate to their land cover. These trees can provide connectivity (Graham 2001), dietary resources (Şekercioğlu et al. 2007), nesting opportunities (Manning et al. 2004; Şekercioğlu et al. 2007), and microclimatic refugia (Şekercioğlu et al. 2007) to many forest species, and can mediate the effects of forest fragmentation (Kupfer et al. 2006).

Despite the ecological importance of shifts in avian function in agroforests and agro-ecosystems, it is surprising that many studies comparing bird communities in forest, agroforest, and agricultural ecosystems do not report on the ecologically important changes in the proportions of avian functional groups, and that such studies report on relative abundance or

estimated biomass even less frequently. Furthermore, as Komar (2006) points out, most coffee studies have failed to sufficiently quantify observer bias or detectability differences between habitats, thus making abundance estimates problematic. Komar also notes that none of these studies has carefully quantified the effects on bird abundance of plantation distance from forest. These criticisms also apply to most studies in other agro-ecosystems. Studies that rigorously compare and manipulate the relative abundance and biomass of avian functional groups in tropical agro-ecosystems, while incorporating landscape effects, comprise a critical frontier in ecology and will help illuminate the ecological causes and consequences of bird community changes in these rapidly expanding, human-dominated landscapes.

This overview has shown that the replacement of forests and agroforests with simplified agricultural systems results in a shift towards less specialized bird communities with altered proportions of functional groups. There is a strong relationship between specialization and extinction risk, and specialized birds are significantly more threatened with extinction (Şekercioğlu 2011). These ecological shifts can affect the ecological functions of and ecosystem services provided by birds in agroforests and other agricultural landscapes. The proportions of insectivores are lower among agroforest and agricultural birds, while the proportions of frugivores and nectarivores, which act as important seed dispersers and pollinators respectively, increase among birds with agroforest habitat preferences, especially in comparison to the bird communities of open agricultural areas. The increased presence of grasses in open agricultural areas contributes to the higher number of granivorous birds, which can become major seed predators and agricultural pests, especially when noncrop species are not producing seeds.

Nevertheless, reduced or increased species richness does not necessarily mean that there will be parallel changes in abundance, biomass, or function (Greenberg et al. 2000b; Perfecto et al. 2004). For example, although insectivorous bird diversity in tropical agroforestry systems is positively related to the magnitude of predator effects, Van Bael et al. (2008) observed no differences between agroforestry systems and forests in the magnitude of bird effects on plant pests, even though agroforest communities have fewer insectivorous bird species, simplified habitat structure, and less plant diversity (Van Bael et al. 2008). Given these uncertainties, there is an urgent need for detailed field studies comparing avian function and functional diversity between forests, agroforests, and simplified agricultural systems, ideally in landscapes that vary in their forest cover and composition.

High biodiversity can be successfully combined with high yields in tropical agroforests (Clough et al. 2011), and Perfecto and Vandermeer (2008)

concluded that “diverse, low-input agroecosystems using agroecological principles are probably the best option for a high-quality matrix.” Diverse, low-input agro-ecosystems include traditional shade coffee and cacao plantations (e.g., Buechley et al. 2015) and a number of other agroforestry types. The findings of these global analyses and reviews indicate that such agroforestry systems with some native cover also maintain a significantly larger proportion of important avian guilds such as frugivores and nectarivores, and a larger proportion of their respective services. These agroforestry systems also harbor substantially lower numbers and proportions of granivorous birds, some of which are major seed and crop predators. Agroforests and other agricultural habitats rich in tree cover are essential for connecting isolated protected areas and their metapopulations. Maintaining diverse, low-input, and preferably traditional agroforestry systems interspersed with tropical forest remnants not only will sustain more native biodiversity in tropical agricultural areas, but will also support higher proportions of avian seed dispersers, pollinators, insect predators, and their valuable ecosystem services. Nonetheless, most forest specialist species are lost from agroforest and open agricultural habitats, so preserving intact forest habitat is likely necessary to conserve much of the diversity of tropical bird communities.

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APPENDIX C

SUBTERRANEAN CACHING OF DOMESTIC COW (*BOS TAURUS*) CARCASSES BY AMERICAN BADGERS (*TAXIDEA TAXUS*) IN THE GREAT BASIN DESERT, UTAH.

Frehner, E.H., E.R. Buechley, T. Christensen, and Ç.H. Şekercioğlu. 2017. Subterranean caching of domestic cow (*Bos taurus*) carcasses by American badgers (*Taxidea taxus*) in the Great Basin Desert, Utah. *Western North American Naturalist* 77(1):124–129.

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SUBTERRANEAN CACHING OF DOMESTIC COW (*BOS TAURUS*)
CARCASSES BY AMERICAN BADGERS (*TAXIDEA TAXUS*)
IN THE GREAT BASIN DESERT, UTAH

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ABSTRACT.—Camera traps documented 2 solitary American badgers (*Taxidea taxus*) independently caching juvenile domestic cow (*Bos taurus*) carcasses during late winter 2016 in the Great Basin Desert of Utah. One carcass was partially buried and the other was entirely buried. Both badgers constructed dens alongside their cache, where they slept, fed, and spent up to 11 days continuously underground. They abandoned the sites 41 and 52 days after initial discovery. While badgers are known to scavenge and to cache small food items underground, this is the first evidence of an American badger caching an animal carcass larger than itself.

RESUMEN.—Cámaras de caza grabaron a dos independientes y solitarios Tejónes Americanos (*Taxidea taxus*) almacenando cadáveres de becerro (*Bos taurus*) a finales del invierno del 2016 en el Desierto del Gran Barreño (Great Basin) de Utah. Uno de los cadáveres de becerro fue enterrado parcialmente mientras que el otro fue completamente enterrado. Ambos tejónes construyeron madrigueras junto a su almacén, donde durmieron, comieron y pasaron once días continuos bajo tierra. Después de este descubrimiento inicial los dos abandonaron sus escondites después de 41 y 52 días. Aunque a los tejónes les conocen por buscar carroña y almacenar alimentos pequeños bajo la tierra, esta es la primera evidencia de un tejón Americano almacenando el cadáver de un animal más grande que el mismo.

The American badger (*Taxidea taxus*) is a midsize fossorial mustelid that ranges throughout western and central North America from northern Alberta, Canada, to central Mexico. It measures 600 to 730 mm in total length (Long 1978) with females weighing an average of 6.3 kg and males an average of 8.6 kg (Lindzey 2003). Badgers are generalist carnivores, whose diets are composed of a wide variety of nutrient sources including carrion and occasional plant material, although their morphological adaptations make them especially adept at excavating underground for small burrowing mammals, which make up the majority of their diet (Jense and Linder 1970, Lindzey 1971, Messick and Hornocker 1981, Goodrich and Buskirk 1998).

Badger morphology is specialized to facilitate scratch-digging and subterranean excavation. Thick protective fur and a conical head equipped with nictitating eyelids, along with stout, heavily muscled forelimbs and long front claws (Moore et al. 2013) facilitate underground hunting and den making. Badgers also use this suite of evolutionary adaptations to their advantage by caching the carcasses of

small mammalian prey, including ground squirrels and jackrabbits, in holes and dirt mounds (Snead and Hendrickson 1942, Lindzey 1971, Michener 2000). Subterranean caching of carrion has been thought to primarily be a strategy to supplement fresh kills and prevent discovery and pilferage of excess food by vertebrate scavengers (Michener 2000, Hüner and Peter 2012) and invertebrates, and to also slow the rate of microbial decomposition through temperature regulation in a cooler underground microclimate (Bischoff-Mattson and Mattson 2009, Inman et al. 2012).

Here we report 2 independent occurrences of American badgers burying carcasses of large animals (domestic cattle) in the Great Basin desert of western Utah during the late winter and early spring of 2016. These events, recorded in detail using camera traps, are the first documentation of this behavior by the American badger.

METHODS

In a study of scavenger ecology in the Great Basin Desert, 7 domestic calf (*Bos taurus*) carcasses were placed on public land managed

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TABLE 1. Site locations (decimal degrees) and elevations.

Site	Latitude	Longitude	Elevation (m)
1	40.891248	-112.951609	1320
2	40.827532	-112.995248	1447
3	40.872537	-113.051194	1433
4	40.758076	-113.090869	1304
5	40.867862	-113.113961	1297
6	40.845341	-113.032534	1409
7	40.894412	-113.000178	1372

by the Bureau of Land Management (BLM) in northwestern Utah. The carcasses were acquired from a local dairy farm in Richfield, Utah. The calves had died from natural causes either during birth or soon after, and were kept frozen until they were placed out for the study. The carcasses weighed between 18.6 and 26.9 kg ($\bar{x} = 22.9$ kg). The carcasses were placed at least 3 km apart (Table 1) in habitat that included sparse Utah juniper (*Juniperus osteosperma*) on higher and hillier sites, greasewood (*Sarcobatus vermiculatus*) in bottoms, and widely distributed cheatgrass (*Bromus tectorum*). The soil in the study area is composed of loose to moderately compacted limnological sediments, including gravels and clays. The carcasses were fixed to a concealed stake in the ground so as to prevent scavengers from dragging off the complete carcass. The carcasses were monitored with Bushnell Trophy Cam HD motion-activated cameras. The cameras were all programmed to take 1 photo when triggered, with a 10-s delay between subsequent photos (the delay is to reduce having multiple photos of the same animal visitation event). The sites were visited every 2 weeks to check equipment and download camera data.

Photos were entered into CameraBase Version 1.7 (Tobler 2007), a camera-trap photo management platform in Microsoft Access. Each photo was viewed to check for the presence of any vertebrates, which were identified to species. All photos containing badgers were examined to compare the pelage patterns of dorsal head stripes and differentiate between individuals as described by Harrison (2016). Because all cameras were programmed to take 1 picture when triggered, with a 10-s delay, the total number of photos of each species can be used as a standardized metric of animal presence at a carcass (Hamel et al. 2013).

RESULTS

Badger activity was observed at 4 of the 7 carcass sites: Sites 1, 2, 3, and 6. At Sites 1 and 2, activity was limited to investigation of the carcass and feeding behavior lasting no more than 2 min. At Site 3, a badger partially buried the carcass, and the carcass at Site 6 was buried entirely (Supplementary Material 1). Both badgers dug burrows alongside the carcasses in which they fed and slept.

The carcasses at both of these sites were placed on 11 January 2016. At Site 3, the badger discovered the carcass on 13 January (Fig. 1). At Site 6, the badger discovered the carcass on 16 January (Fig. 2). Sites 3 and 6 were located 3.4 km apart, and the badgers were photographed near simultaneously at the 2 different sites. Furthermore, inspection of pelage patterns showed no evidence that more than a single solitary badger visited each of the 2 sites through the duration of the study. Both badgers inspected the carcasses and the surrounding area for <2 min on their first visit. They each exhibited their first feeding behavior the day following initial discovery, tearing at the underbelly and the back of the carcasses, respectively.

At Site 3, the badger returned intermittently to feed on the carcass over the course of several days following its discovery, tearing a large opening in the carcass's lower abdomen and feeding on internal organs. This behavior occurred from 15 January through 17 January, at which point the badger was first seen digging around the carcass in an episode that lasted from 14:06 to 14:15. After this point, the badger began to return twice daily to dig for 10–20 min at a time—once in the early morning between 01:00 and 03:00, and once between 11:00 and 12:30. The badger would stop occasionally during these episodes to feed upon the carcass. This pattern continued until 19 January, when a portion of the badger's subterranean excavation collapsed, causing the hindquarters of the carcass to fall into the badger's hole.

On 21 January, the badger at Site 3 began residing in a den that it had constructed alongside the carcass, after which point it spent the majority of its time underground until 17 February. During this time, the badger rarely left the immediate vicinity of the partially buried carcass, emerging from the hole only to

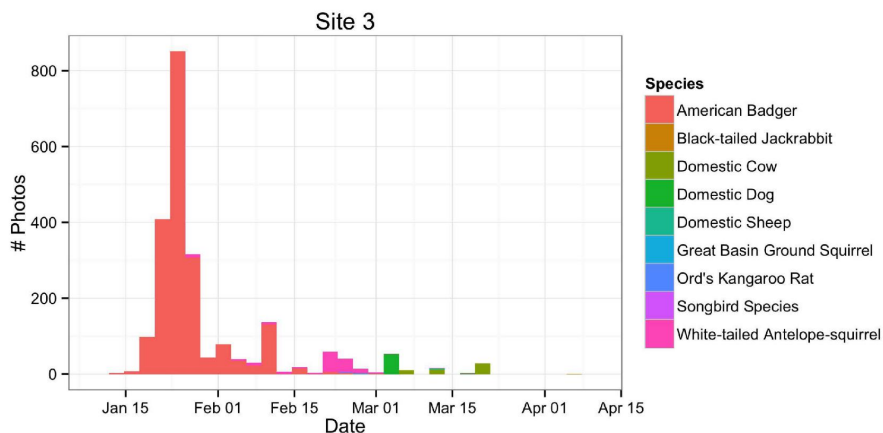


Fig. 1. Vertebrate camera-trap photograph captures at Site 3.

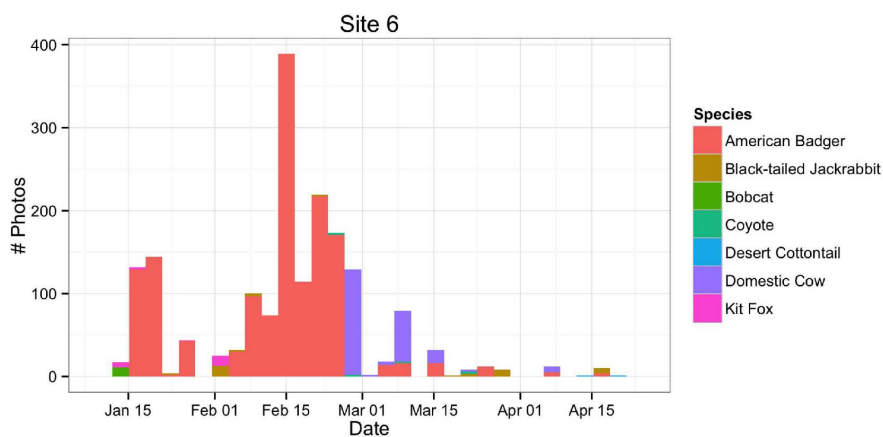


Fig. 2. Vertebrate camera-trap photograph captures at Site 6. The arrival of domestic cows appears to have caused the badger to abandon its den site at the carcass.

inspect the area around the entrance of the burrow and attempt to maneuver the carcass the rest of the way into its hole—though the anchoring stake prevented the badger from ever accomplishing this. On 28 January and 5 February, the badger did not emerge from its burrow at all, staying underground for 28 h and 33 h, respectively. On the morning of 7 February, the badger left the burrow and did not return for 72 h, and even then only stopped for 13 min to feed at the entrance

of the burrow. The badger returned twice more for visits lasting no more than 10 min on 16 February and 21 February, and was not seen again after that.

The badger at Site 6 invested a considerable effort in burying the carcass in the days immediately following its initial discovery on 16 January. It excavated below and around the carcass from 18:03 to 22:24 on 17 January, with only a single pause to feed, which lasted for 5 min. It resumed digging the following

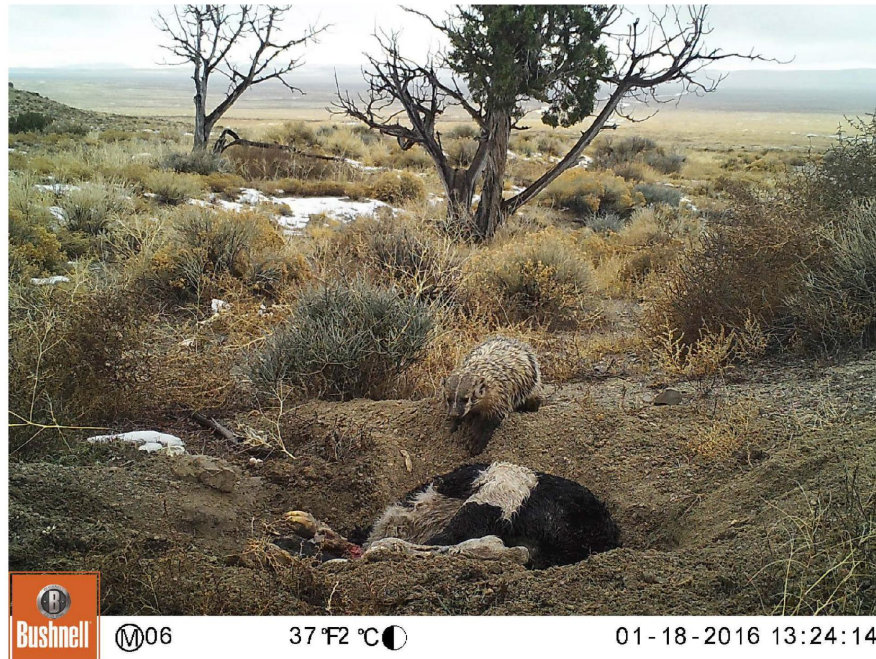


Fig. 3. An American badger (*Taxidea taxus*) actively burying a juvenile domestic cow (*Bos taurus*) carcass at Site 6 in the Great Basin Desert of northwestern Utah.

afternoon, 18 January, at 13:10, and by 13:24 a tunnel had collapsed, bringing the entire carcass down with it and leaving the carcass approximately half submerged (Fig. 3). The badger continued to dig until 16:15, by which time the carcass had fallen further down into what was at that point a substantial hole measuring approximately 70 cm deep and nearly 2 m in diameter. The badger then made an effort to partially cover the carcass with dirt and left shortly thereafter at 16:19.

When the badger returned at 9:55 on the morning of 19 January, there had been another collapse within the excavation that left a crater into which the carcass had completely disappeared. After this point, the badger spent the majority of its time in or around the hole, leaving the immediate vicinity of the carcass only sporadically and for increasingly short amounts of time. The badger instead put its time into backfilling over the carcass and leveling the ground where it had

been, leaving only a small entrance to its subterranean cache. By 21 January, the badger had appeared to fully move into a burrow next to the carcass, and until 6 February, it spent the majority of its time underground. It came to the entrance for approximately 2 min on 23 January and left the site for 3 h on 25 January and 5 h on 6 February.

On 7 February, the badger emerged from its hole at 11:02, covered the entrance to its hole with dirt, and left the site. It didn't return until the following night, 8 February, at 20:18, at which point it uncovered the entrance and reentered the hole. It re-emerged the morning of 9 February at 11:59, reburied the entrance, left the site, and returned that afternoon at 14:45. From this point on, until 25 February, the badger spent the majority of its time in the burrow or rolling around in the dirt immediately outside of the entrance. It made only occasional trips off-site, covering the entrance before

leaving for anything more than half an hour at a time.

On 25 February, the badger left the site at 13:51. A herd of domestic cows came into the area later that day at 20:55, and they occupied the site until 17:27 on 29 February. There were no photos of them at the site after 29 February and no photos of the badger returning until 4 March. Following its return, the badger spent most of the next 2 days in the burrow, but after cows again passed by the site at 12:30 and 15:04 on 6 March, the badger appeared agitated, repeatedly entering and exiting the den and pacing in circles around its entrance. On 8 March, the badger left the site, leaving its den for the last time. Over the next 3 months there was substantial cattle activity at and around Site 6, and though a badger made visits of no more than 10 min to the site on 16 March and 24 March, and 7 April and 16 April, it never reentered the burrow.

During the study, the badgers at both Site 3 and Site 6 were active during all hours of the day, though both had a peak in their activity levels in the middle of the day between 10:00 and 13:00. This is somewhat surprising, considering the species' typically nocturnal habits. Once the badgers had established themselves at these sites, observed activity of other species decreased substantially compared to the other 5 sites in the study. At Site 3, there were only occasional visitations of the site by white-tailed antelope squirrels (*Ammospermophilus leucurus*) during the badger's presence, with the rodents approaching the mouth of the burrow in order to retrieve fur from the carcass (presumably to be used as nesting material). At Site 6 there were photographs of passing black-tailed jackrabbits (*Lepus californicus*) and brief investigative visits by a solitary bobcat (*Lynx rufus*), kit fox (*Vulpes macrotis*), and coyote (*Canis latrans*) prior to the arrival of domestic cows at the site, which appears to have caused the badger to abandon its burrow.

DISCUSSION

To our knowledge, this is the first documented account of an American badger—or any other mustelid—burying an immovable carcass significantly more massive (3–4 times) than itself. Several North American mustelid species, including the wolverine (*Gulo gulo*), marten (*Martes americana*), and long-tailed

weasel (*Mustela frenata*) have been known to cache carcasses of ungulates and rodents (Henry et al. 1990, Muths 1998, Inman et al. 2012), and a study by Hüner and Peter (2012) described a fisher (*Martes pennanti*) caching an American black bear (*Ursus americanus*) carcass *in situ* beneath branches and bracken (but not burying it). Though American badgers have previously been documented feeding on large mammalian carrion, such as domestic pig (*Sus scrofa domesticus*) and cattle (*Bos taurus*) (Snead and Hendrickson 1942, Sovada et al. 1999), there have been no previously published records of badgers caching items larger than jackrabbits (Snead and Hendrickson 1942, Lindzey 1971, Michener 2000).

American badger activity in this study has demonstrated that badgers are capable of caching carcasses weighing over 20 kg; they would thus likely be able to bury the majority of carrion items that they encounter in the wild. This is ecologically significant as American badgers are widespread mammals that could be responsible for consuming a much larger portion of carrion in many ecosystems than previously thought, potentially having a significant impact on nutrient cycling across their large geographic range. Furthermore, the burial of diseased carcasses could provide a significant ecosystem service to ranchers.

SUPPLEMENTARY MATERIAL

One online-only supplementary file accompanies this article (scholarsarchive.byu.edu/wnan/vol77/iss1/13).

SUPPLEMENTARY MATERIAL 1. Time-lapse video of Site 6, showing a solitary badger completely burying the carcass of a juvenile cow.

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APPENDIX D

IMPORTANCE OF ETHIOPIAN SHADE

COFFEE FARMS FOR FOREST

BIRD CONSERVATION

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Special Issue Article: Tropical Insectivores

Importance of Ethiopian shade coffee farms for forest bird conservation

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ABSTRACT

Coffee is the most important tropical commodity and is grown in high-priority areas for biological conservation. There is abundant literature on the conservation value of coffee farms internationally, but there has been little research on this topic in Africa. Ethiopia is a diverse and little-studied country with high levels of avian endemism, pressing conservation challenges, and where *Coffea arabica* originated. We sampled bird communities in shade coffee farms and moist evergreen Afromontane forest in Ethiopia utilizing standard mist netting procedures at seven sites over three years to evaluate bird species richness, diversity and community structure. Although species diversity did not differ between shade coffee and forest, shade coffee farms had over double the species richness of forest sites and all but one of the nine Palearctic migratory species were captured only in shade coffee. There was a greater relative abundance of forest specialists and understory insectivores in forest, demonstrating that little-disturbed forest is critical for sustaining these at-risk groups of birds. Nonetheless, all species recorded in primary forest control sites were also recorded in shade coffee, indicating that Ethiopian shade coffee is perhaps the most “bird-friendly” coffee in the world. This is an important finding for efforts to conserve forest birds in Africa, and for shade coffee farmers that may benefit from avian pest regulation and biodiversity-friendly coffee certifications.

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1. Introduction

1.1. Tropical forest declines and implications for bird populations

Increasing human populations and corresponding land use changes are driving a global extinction crisis (Brashares et al., 2001; Pimm et al., 2006; Vitousek et al., 1997). Tropical forests are the most species-rich terrestrial ecosystem on Earth, supporting up to 70% of plant and animal species, and are being lost at an alarming rate (Dirzo and Raven, 2003; Donald, 2004; Laurance and Bierregaard, 1997; Sodhi et al., 2004). In the last decade, approximately 13 million hectares of forest were cut down each

year, with most of the losses occurring in the tropics (UNFAO, 2010). Tropical deforestation represents the single greatest threat to global biodiversity (Donald, 2004): it results in rapid transformations in plant and animal communities, which drastically alters ecological processes and impacts human societies (Clough et al., 2009a; Tilman et al., 2001).

Numerous studies attribute forest bird declines to deforestation and the conversion of tropical forests to agricultural habitats, particularly in forest archipelagos in agricultural landscapes (Bregman et al., 2014; Newmark, 1991; Şekercioğlu, 2012a; Sigel et al., 2006; Sodhi et al., 2011; Stratford and Stouffer, 1999). Currently, 23% of bird species are globally threatened or near threatened with extinction (BirdLife International, 2014), with the vast majority of threatened species inhabiting tropical forests (BirdLife International, 2014; Brooks et al., 1999; Lees and Peres, 2006; Sodhi et al., 2004; Turner, 1996).

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Understanding the ecological drivers underlying avian distributions is critical to evaluate the overall ecological integrity of ecosystems because birds are highly specialized, occupy a variety of ecological niches, have key ecological functions, and are variably susceptible to disturbance (Komar, 2006; Şekercioğlu, 2006a, 2006b; Anjos et al., 2015; Pollock et al., 2014; Pavlacky et al., 2014). Bird extinction risk increases with ecological specialization (Şekercioğlu, 2011). Shifts in bird relative abundance and/or local extinctions are likely to affect ecological processes, including seed dispersal, pollination, nutrient cycling, and even soil formation (Chapin et al., 1998; Heine and Speir, 1989; Lens et al., 2002; Şekercioğlu et al., in press).

Forest understory insectivores are especially sensitive to forest fragmentation and disturbance, and are thus among the most threatened bird species in the world (Tobias et al., 2013). They have relatively high habitat specificity, dependence on forest interior habitats, and limited mobility (Lens et al., 2002; Şekercioğlu et al., 2002; Tobias et al., 2013). Evaluating where and why they are declining is a conservation priority in the tropics (Tobias et al., 2013).

1.2. Agroforests as bird habitat

Preserving biodiversity in habitats that are impacted by human activities is important because (i) these habitats make up an increasingly large portion of the globe (Norris, 2008) and (ii) about one third of the world's ~10,000 bird species have been recorded in human-dominated and mostly agricultural habitats (Şekercioğlu et al., 2007). Agriculture accounts for over 37% of global land cover (World Bank, 2012a) and is a major cause of deforestation. Agroforestry—a farming technique that combines a mixture of trees, shrubs, and crops—is particularly valuable for biodiversity conservation, especially when native tree species are present (Fischer and Lindenmayer, 2007; Perfecto et al., 1996; Pimentel et al., 1992). The conservation value of tropical agroforests is being increasingly recognized (Greenberg et al., 2008; Perfecto and Vandermeer, 2008; Tschamtkle and Klein, 2005). Landscape management strategies that maximize biological diversity retention, ecological services, and economic profitability should be investigated and promoted (Bengtsson et al., 2005; Railsback and Johnson, 2014; Rosenzweig, 2003).

A number of factors affect bird assemblages in tropical agroforests, including forest patch size, proximity to other habitat types, percent canopy cover, and shade tree composition. For example, agroforests that have intact forest canopies with high shade tree diversity and native tree species harbor relatively high avian diversity (Gove et al., 2008; Perfecto et al., 1996; Greenberg et al., 1997; Van Bael et al., 2007). Shade coffee is among the most bird-friendly of agricultural habitats, often harboring a high diversity of birds, including forest specialists (Komar, 2006; Perfecto et al., 1996; Greenberg et al., 1997; Van Bael et al., 2007). However, most avian studies only evaluate species diversity or richness, and often overlook the role of community composition in shaping the ecological and conservation importance of bird species utilizing coffee farms. In particular, there is a need to evaluate the degree of habitat specialization, foraging guild structure, and conservation status of bird communities (Komar, 2006). Furthermore, the majority of this research has taken place in the Neotropics and the ecology of birds in coffee farms in Africa, in particular, needs further investigation (Komar, 2006; Şekercioğlu, 2012a).

1.3. Ethiopia: Importance and challenges

Ethiopia is a unique, immensely diverse and little-studied country with a high level of avian endemism. It is located along the critical African-Eurasian migratory flyway (Ash et al., 2009;

Şekercioğlu, 2012b). Eastern Afromontane and Horn of Africa Global Biodiversity Hotspots cover most of the country (Conservation International, 2014) and the Ethiopian highlands account for over 50% of the Eastern Afromontane eco-region (Fig. A1). This eco-region is intermittently distributed, is the least explored and least protected eco-region in Africa, and is a major source of endemism (Gole et al., 2008; Küper et al., 2004; Scholes et al., 2006). Approximately three-quarters of plant species (Gole et al., 2008) and 32 bird species are endemic to the Abyssinian Highlands, which include Ethiopia and a portion of neighboring Eritrea (Ash et al., 2009). Despite minimal visitation by ornithologists and birders, especially the unstable border regions with Somalia, Kenya, North and South Sudan, and Eritrea, an impressive total of over 860 species have been documented (Şekercioğlu, 2012b); ranking Ethiopia among the richest countries in the world in terms of bird diversity. This species list is steadily growing with increasing research and tourism. The combination of bird diversity, endemism, globally important migration routes, and scant research make Ethiopia a top priority in Africa for ornithological research and conservation (Şekercioğlu, 2012b).

While Ethiopia has a tremendous wealth of natural resources and biological diversity, it also faces serious conservation challenges. The country's population growth rate is among the highest in the world—currently estimated at 2.6% per year (World Bank, 2013)—which is causing rapid and widespread conversion of forest habitats for human settlements, charcoal and firewood harvesting, and clearing for agriculture, including tea and coffee plantations (Bekele, 2011; Campbell, 1991; Hurni, 1988). Furthermore, there is limited governmental commitment to wild-land conservation. These factors have led to widespread deforestation in the biologically rich Ethiopian highlands: forest cover was reduced from over 15,100,000 ha in 1990 to just under 12,300,000 ha in 2010—a drastic 18.6% decline in 20 years (FAO, 2010).

Global coffee consumption has increased consistently since the early 1980s, at a rate of about 1.2% annually (ICO, 2012a). With an annual value of \$100 billion (Donald, 2004), coffee is the second most valuable legal international commodity after oil (O'Brien and Kinnaird, 2003) and is the most important export commodity for many tropical countries (ICO, 2012a). It is produced on approximately 11.5 million hectares of terrain, often in areas of high conservation importance (Donald, 2004). *Coffea arabica*—the most widespread and economically valuable coffee strain—makes up two-thirds of the world's coffee market (Aerts et al., 2011; Labouisse et al., 2008), and is native to southwestern Ethiopia where it has been cultivated for over a thousand years (Aerts et al., 2013; Anthony et al., 2001, 2002).

The agricultural industry accounts for 80% of employment in Ethiopia (United Nations, 2012) and coffee is the primary export crop (ICO, 2012b). From 2000 to 2010, coffee accounted for an average of 33% of export earnings, the second most of any country (ICO, 2012b). Present day coffee cultivation in Ethiopia ranges from the harvesting of near-wild coffee in forest to shade coffee farms with native tree canopies to monoculture sun coffee farms. While Ethiopia has a long history of shade coffee farming, it is following a recent global trend towards sun coffee production, due to the ease of mechanization which can yield higher production per unit area despite decreased production per plant (Donald, 2004; Gove et al., 2008). Intensive sun coffee farms produce a lower quality crop and often face problems with crop pollination and pest outbreaks due to loss of avian ecological function (Kellermann et al., 2008). These biodiversity losses can cause increased reliance on pesticides, which in turn cause further ecological damage (Donald, 2004). As little forest cover remains in Ethiopia and agriculture is the dominant land use, determining the conservation value of agricultural systems is pressing. In addition to being an important step towards determining avian conservation priorities

in the tropics, our study also fills an important gap in the existing literature on birds in coffee farms, in a country with high levels of biodiversity, endemism, deforestation rates, human population growth, and economic dependence on agriculture.

2. Material and methods

2.1. Site description

Our study took place in the Oromia Region of southwestern Ethiopia, in the heart of the country's coffee producing region and where *C. arabica* was first domesticated from wild stock (Anthony et al., 2002). Bird community sampling was carried out in two habitat types: shade coffee farms (422 km² area; at four localities, Garuke, Eladale, Fetche, and Yebu) and moist evergreen Afromontane forest (920 km² area; at three localities, Afalo, Abana Buna, and Qacho) (Fig. 1).

The shade coffee farms are located within the major coffee-producing agricultural mosaic near the city of Jimma (in Kaffa Province, which gave coffee its name) and are all operated by small-scale local farmers with similar growing strategies. The area of the shade coffee farms ranged from two to ten hectares. These shade coffee farms are agroforest fragments in a patchwork of pastures and agriculture. There is extensive canopy and understory thinning and widespread planting of *C. arabica* at high densities and regularly spaced intervals. The coffee cultivars at all of the sites were from wild stocks of *C. arabica* and there was no documented pesticide or fungicide use on the farms. The shade coffee sites have a simplified structure and reduced shrub and tree species

composition when compared with the forest sites. Three forest sites were selected from the closest accessible large contiguous forest patches that occurred within the same elevational range, climatic region, and vegetation zone as our shade coffee sites. Located within the Belete-Gera Regional Forest Priority Area, these sites showed only moderate signs of forest management and human alteration, including some clearing of the understory to promote the growth of wild coffee. The forest was complex structurally and compositionally, including diverse herbs, shrubs, lianas and saplings, with an average canopy height of approximately 20 m in the most pristine sections.

Hundera et al. (2013) studied forest composition and structure within our same study sites in detail. They documented a total of 69 woody plant species across all sites, with 44 species found in forest, while 26–38 species were found on different shade coffee farms. When comparing forest to shade coffee, there was a 70–95% reduction of seedlings, tree abundance was reduced by 30–68%, and basal area decreased by up to 75%, respectively. Emergent tree species, such as *Pouteria adolfi-friederici*, *Olea welwitschii*, and *Afrocarpus falcatus*, are often the first removed in the conversion from forest to shade coffee. While mean tree and canopy height did not vary significantly between habitats, regeneration of late successional tree species was significantly greater in forest than in shade coffee. Hundera et al. (2013) conclude that cutting of saplings in shade coffee inhibits recruitment of late-successional and secondary tree species.

We determined the elevation and mean annual rainfall for all study localities (Table A1). Elevation was extracted from a high resolution digital elevation model (Hijmans et al., 2005), and rainfall values were determined using a world climate database

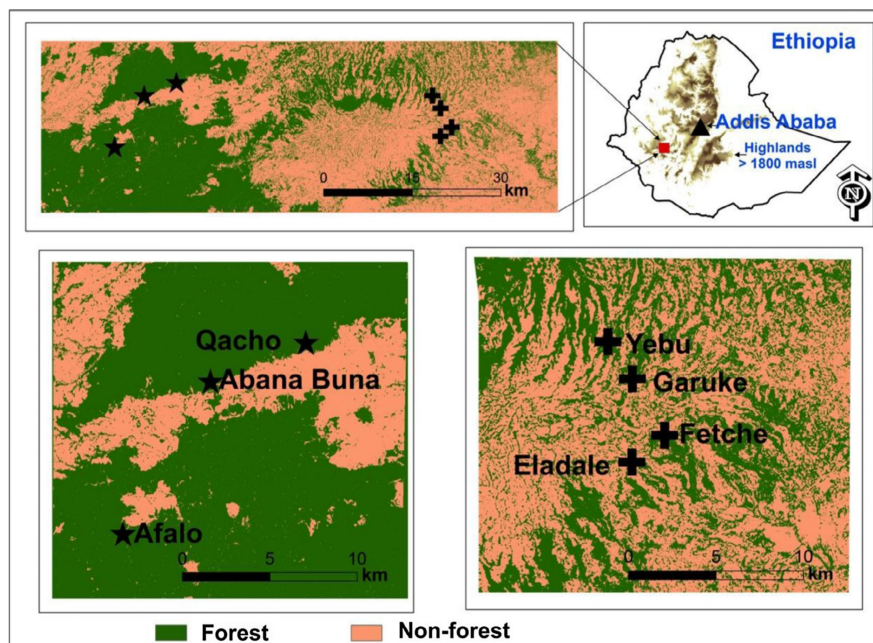


Fig. 1. Location of four shade coffee farms (+) and three moist evergreen Afromontane forest sites (★) where mist netting took place in southwestern Ethiopia. The map shows regional forest cover from a 30 m resolution Landsat image (WorldClim.org, 2014) and classified using ERDAS Imagine Software (Leica Geosystems, 2004).

(WorldClim, 2014). All study sites are located in a 110 m elevational band. The sites are at least 3 km apart and the maximum distance between the two most distant localities is 57 km. All sites occur within the Moist Evergreen Montane Forest vegetation zone and the Warm Temperate 1 and 2 climatic regions as described in Ash et al. (2009). There are distinct weather seasons in the region; a wet season from March to mid-September, with peak rains occurring in April and August, and a dry season from September to February.

2.2. Study design and sampling

Birds were sampled at all sites using standard mist-netting procedures as described in Karr (1979). Mist-netting is regarded as an effective method for sampling understory bird communities, as it can detect species that are cryptic and/or less vocal and is repeatable with few observer biases (Karr, 1981). Sampling took place during the dry season, from December to February, over a three-year time frame, from 2010 to 2012. At each site, we positioned twenty 12×2.5 m nets within a 1 ha area and at least 50 m from any bordering habitat type. As much as the terrain and vegetation allowed, net placement approximated a square of 60 m on each side. We used the same net lanes throughout the three-year study period. Each site was sampled at least six times every season, with approximately two weeks between each sampling session. A sampling session consisted of opening the nets half an hour before sunrise and keeping the nets open for six continuous hours. The nets were routinely checked at 30-min intervals so as to promptly remove, process, and release the birds. To process each bird we identified the species, banded it, took standard measurements, and released it (Redman et al., 2009; Stevenson and Fanshawe, 2002).

2.3. Bird classification

We classified each bird species using four main criteria: (i) migratory status, (ii) forest dependence, (iii) foraging guild, and (iv) habitat strata association. Bird taxonomy follows Clements' 6th Edition, updated in 2014 (Clements, 2014).

We first classified each species as either a Palearctic migrant or an Afrotropical resident. We then used the established classification of East African forest birds (Bennun et al., 1996) to create a forest dependence rank. In this work, species are classified as forest specialists (FF), forest generalists (F), and forest visitors (f). For a small number of study species that were not included in Bennun et al. (1996), we followed the authors' methods to classify species, using habitat association information found in Ash et al. (2009), del Hoyo et al. (1992), and Redman et al. (2009).

Bird species' foraging guilds were determined using a dataset containing the ecological traits of all of the bird species in the world (hereafter "Birdbase"), as described in Şekercioğlu et al. (2004). This dataset was initially compiled from an extensive literature survey of 248 sources, is updated regularly, and has been used in numerous ecological studies and meta-analyses of bird populations (e.g. Bregman et al., 2014; Burivalova et al., 2014; Redding et al., 2015; Şekercioğlu, 2012a). Herein, seven food categories are identified (plant material, seeds, fleshy fruits, nectar, invertebrates, carrion, and vertebrates) and ordered by priority in each species' diet on a ten-point scale to determine primary diet and foraging strategy. The species' first diet choice was used to classify it into one of the following guilds that were present in our study: frugivore, nectarivore, granivore, and insectivore. Consulting the Birdbase, Ash et al. (2009), del Hoyo et al. (1992), and Redman et al. (2009), we also categorized each species' occurrence within the understory, midstory, and canopy.

Using these categories, we identified two additional groups: understory insectivores, and resident understory insectivores. These groups are composed of species that are insectivorous and consistently frequent the understory, with the latter including only Afrotropical resident species. These groups are of particular interest in this study for two main reasons: (i) pan-tropical studies have shown that understory insectivores are highly impacted by forest modifications (e.g. Bregman et al., 2014; Burivalova et al., 2014), making them good indicators of forest health; (ii) understory insectivores have been shown to contribute ecosystem services to coffee farmers in the form of pest-regulation in other regions of the world (Şekercioğlu et al., in press), and may likewise be of economic importance to coffee farmers in Ethiopia. (See Table A2 for a list of species along with their classifications included in the analysis.)

2.4. Data analysis

We made several modifications to the dataset prior to analysis, to account for limitations and potential biases associated with mist net data (Remsen and Good, 1996) (see Section 4 for full treatment of these issues). We removed species that do not consistently frequent the understory and species that are not reliably caught in mist nets due to their large size, such as raptors, owls, and ravens (Wang and Finch, 2002; see Table A3 for a list of species and the reason they were excluded from the analysis). Individuals were only counted when trapped first (recaptures were excluded from the analysis) to avoid estimation bias from individuals that were recaptured many times (Remsen and Good, 1996). Then, all shade coffee sites and forest sites were combined, so as to compare the two major habitat types.

Using EstimateS 9.1.0 (Colwell, 2013), we calculated estimated species richness $S(\text{est})$, estimated shared species $V(\text{est})$, and Morisita–Horn sample similarity. We used the Chao1 estimator to calculate $S(\text{est})$ for our species relative abundance data. The Morisita–Horn index was used because it has minimal sample size biases and is useful for large species assemblages with many rarely recorded species, as was the case in our study (Magurran, 1988). Rarefaction and extrapolation curves of $S(\text{est})$ were computed with 95% confidence intervals in both habitat types, extrapolating the smaller sample to the number of captures of the larger sample (1208 individuals), in order to directly compare observed and estimated species richness in both habitats. Using this method, statistically robust extrapolation of samples is possible to directly compare sites with different sample sizes, as was the case in our study (Colwell et al., 2012).

Shannon's Diversity (H) was compared between forest and shade coffee by fitting a generalized linear mixed effects model using the package lme4 in R (Bates et al., 2008). Average Shannon's Diversity for each one of the 142 sampling sessions from the seven sites was used as the response variable, site as the random effect and habitat (shade coffee or forest) as the fixed effect. The frequency of breeding birds was determined for both habitats, using the number of individuals in breeding condition, as evidenced by cloacal protuberance or brood patch, divided by the total number of captures (Ralph and Dunn, 2004). The ratio of juvenile to adult birds was then determined. Birds in their first year were classified as juveniles and all birds in their second year or after were classified as adults, with species of undetermined age excluded. Relative abundance was determined from the capture rate (number of birds per net hour), an index which controls for differing effort between habitats (Karr, 1982; Newmark, 1991). To compare relative abundance between habitats, we (i) identified the capture rate of each individual species and each bird classification category and (ii) divided this by the total capture rate in each habitat respectively. We then ran a chi-square analysis in SPSS 21.0 (IBM Corp., 2012)

to test for significant differences in relative abundance between habitats.

3. Results

3.1. Bird captures, richness and diversity

A total of 1692 individuals of 71 species were captured in 18,177 net-hours; 1281 individuals were captured in shade coffee and 411 in forest. Nine species were excluded from analysis due to their large body sizes and 11 species were excluded because they do not consistently frequent the understory. After these refinements to the dataset were made, 1605 individuals (94.9% of all individuals captured) of 51 species (71.8% of all species captured) were included in the analysis. All 51 species were captured in shade coffee, while 19 of these were caught in forest. Because shade coffee had more land cover, mist netting effort in shade coffee (13,690 net hours) was more than double the effort in forest sites (4487 net hours), while the overall capture rate was identical (0.085 and 0.082 birds per net-hour in forest and shade coffee, respectively). Six species had significantly greater relative abundance in forest, as determined from the capture rate: Lemon Dove (*Columba larvata*), African Hill Babbler (*Sylvia abyssinica*), Abyssinian Ground-thrush (*Geokichla piaggiae*), Eastern Olive Sunbird (*Cyanomitra olivacea*), Abyssinian Crimson-wing (*Cryptospiza salvadorii*) and Green-backed Twinspot (*Mandingoa nitidula*). Nine species had significantly greater relative abundance in shade coffee: Tambourine Dove (*Turtur tympanistria*), Yellow-fronted Tinkerbird (*Pogoniulus chrysoconus*), Willow Warbler (*Phylloscopus trochilus*), Blackcap (*Sylvia atricapilla*), Common Chiffchaff (*Phylloscopus collybita*), Broad-ringed White-eye (*Zosterops poliogastrus*), Abyssinian Slaty-Flycatcher (*Melaenornis chocolatinus*), African Paradise-flycatcher (*Terpsiphone viridis*), and Tree Pipit (*Anthus trivialis*). Palearctic migrants were predominantly found in shade coffee, where they were captured nearly twice as frequently. All but one (Blackcap, *S. atricapilla*) of the nine migratory species were captured only in shade coffee. (See Table A3 for a full list of species included in the analysis with relative abundance values.)

The sites had estimated understory bird species richness $S(\text{est})$ of 51.00 (95% CI [44.49, 57.51]) and 19.25 (95% CI [17.82, 20.67]), for shade coffee and forest, respectively. While sharing an observed 19 species $V(\text{obs})$, estimated shared species Chao $V(\text{est})$ was 20.96. Despite the large difference in species richness between habitats, the Morisita–Horn Sample Similarity Index was 0.728, indicative of a high degree of overlap in bird communities. Species rarefaction and extrapolation curves reached a plateau in forest, while shade coffee curves had a positive slope indicating that continued sampling in this habitat might have yielded additional species

(Fig. 2). Analysis of Shannon's Diversity Index showed no significant difference in bird diversity between shade coffee farms and forest (Table A4).

3.2. Community structure analysis

While there were no significant differences in overall bird diversity values between shade coffee and forest, there were differences in the relative abundance of bird community categories, as determined from the capture rate.

Forest generalists (F) were frequently captured in both habitat types, accounting for 58% of captures in shade coffee and 41% of captures in forest. Forest visitors (f) accounted for over one-third of all captures in shade coffee, whereas they were only one-fifth of captures in forest. There was no significant difference in the composition of these 2 groups between habitats, however. Importantly, though, forest specialists (FF) had a greater relative abundance in forest than in shade coffee by a wide margin; they were captured nearly 5 times as frequently in this habitat ($\chi^2 = 9.877$, $df = 1$, $p = 0.001$) (Fig. 3).

Four foraging guilds were found in our study: frugivore, granivore, insectivore, and nectarivore. Frugivores had a greater relative abundance in shade coffee ($\chi^2 = 4.670$, $df = 1$, $p = 0.017$), whereas granivores had a greater relative abundance in forest ($\chi^2 = 18.900$, $df = 1$, $p < 0.001$). Nectarivores constituted less than 1% of all captures, with no significant difference between habitats. Insectivores were by far the most frequently captured in both habitats, comprising 68% of all captures in shade coffee and 64% in forest. There was no significant difference in the overall relative abundance of insectivores between the habitats. However, both understory insectivores ($\chi^2 = 14.195$, $df = 1$, $p < 0.001$) and resident understory insectivores ($\chi^2 = 48.392$, $df = 1$, $p < 0.001$) had greater relative abundance in forest. In contrast, shade coffee sites had greater relative abundance of Palearctic migrants ($\chi^2 = 21.375$, $df = 1$, $p < 0.001$) (Fig. 3).

There was no significant difference in the frequency of breeding birds (as evidenced by cloacal protuberance or brood patch) between forest and shade coffee, with 27% of all captures in breeding condition in shade coffee and 23% in forest ($\chi^2 = 2.476$, $df = 1$, $p = 0.065$). The species that most frequently showed signs of breeding in shade coffee were Yellow-fronted Tinkerbird (*P. chrysoconus*), Green-backed Camaroptera (*Camaroptera brachyura*), Broad-ringed White-eye (*Z. poliogastrus*), and Eastern Olive Sunbird (*C. olivacea*). The species that most frequently showed signs of breeding in forest were two of the same species, Broad-ringed White-eye (*Z. poliogastrus*) and Eastern Olive Sunbird (*C. olivacea*), plus African Hill Babbler (*S. abyssinica*) and Abyssinian Crimson-wing (*C. salvadorii*). The juvenile to adult ratio was 0.19 in shade

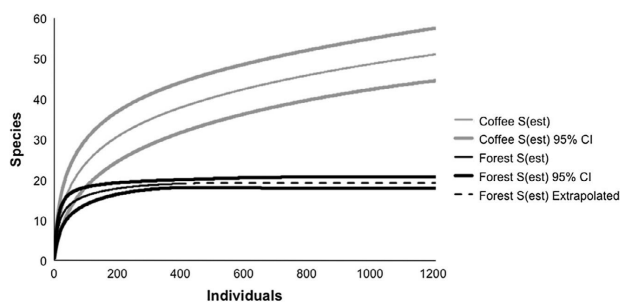


Fig. 2. Observed and extrapolated bird species accumulation curves ($S(\text{est})$) with 95% confidence intervals (CI) for shade coffee farms and moist evergreen Afromontane forest sites in southwestern Ethiopia.

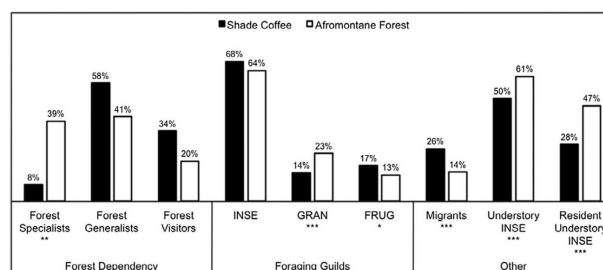


Fig. 3. Summary of the differences in bird relative abundance between shade coffee farms and moist evergreen Afromontane forest sites in southwestern Ethiopia. Bars illustrate the relative abundance of each bird classification category, calculated as the capture rate (# of birds/net hour) in each habitat divided by the total capture rate. Asterisks indicate significant differences in the relative abundance of a category between habitats at the $p < .05$ (*), $p < .01$ (**), and $p < .001$ (***) levels, based on chi-square analysis. Nectarivores were not included in the figure because they accounted for only a fraction of a percent of all captures.

coffee and 0.22 in forest, with no significant difference between sites ($\chi^2 = 2.215$, $df = 1$, $p = 0.080$).

4. Discussion

4.1. Richness and diversity

Results from rarefaction show that shade coffee had over double the species richness of forest. Despite this, the Morisita–Horn Sample Similarity Index indicates high community overlap of nearly 73% between the bird communities. There were no significant differences in Shannon's Diversity. Eight of the nine Palearctic migrants in the study were found only in shade coffee. These results are consistent with numerous tropical studies showing that shade coffee farms harbor high bird species richness and diversity, and provide important habitat for temperate migrants (Jones and Ramoni-Perazzi, 2002; Komar, 2006; Perfecto et al., 2003; Sherry, 2000). The fact that every species we captured in forest was also captured in shade coffee indicates that forest specialist birds may use shade coffee farms in Ethiopia even more than they do in other regions of the world. This is supported by the result that shade coffee had no significant difference from forest in the frequency of birds in breeding condition or the ratio of juveniles to adults. We captured several forest specialist birds in breeding condition in shade coffee, indicating that this habitat may provide viable breeding habitat for some forest specialists, including Lemon Dove (*C. larvata*), Abyssinian Ground-thrush (*G. piaggiae*), Eastern Olive Sunbird (*C. olivacea*), and Green-backed Twinspot (*M. nitidula*). The lack of chemical use in these traditional, organic shade coffee plantations is also likely to contribute to high bird diversity and abundance. However, the viability of shade coffee as breeding habitat for forest birds in this region requires further study. It is possible that shade coffee farms serve mainly as stepping stones for forest birds searching for more suitable habitat, or that these shade coffee fragments are an ecological trap (Battin, 2004) for forest bird species in a highly fragmented and human-dominated landscape. Long-term studies of population dynamics using capture-mark-recapture methods are needed. Nonetheless, the high species richness, diversity, and presence of forest specialist species in organic shade coffee farms in this region are encouraging findings, illustrating the potential importance of shade coffee farms for bird conservation in Africa.

4.2. Community structure

Considering species richness alone, however, could be misleading when assessing the importance of shade coffee farms and forest

for bird conservation. Results from community structure analysis show that there are significant differences in the relative abundance of bird species between the two habitats, illustrating the importance of little-disturbed Afromontane forest for particular groups of birds. For example, forest had a much higher relative abundance of forest specialists, understory insectivores, and resident understory insectivores. These results corroborate studies from around the world that have shown that understory insectivores are among the most susceptible of groups to forest disturbance and are often the first species to disappear from altered forests (Şekercioglu et al., 2002; Stouffer and Bierregaard, 1995; Sodhi et al., 2011; Cordeiro et al., 2015; Pavlacky et al., 2014; Arcilla et al., 2015). In order to conserve forest specialists and understory insectivores in the long term, it is necessary to conserve areas of little-disturbed forest in the Afrotropics as well.

With regard to guild structure, insectivores made up a similar proportion of the community in both forest and shade coffee, a result that is unusual (Hernandez et al., 2013; Şekercioglu, 2012a). This may be explained by the fact that coffee is a native crop within our study area and a larger portion of the invertebrate prey base for insectivores may be maintained in shade coffee farms here. Furthermore, the lack of chemical use also favors insectivorous birds. A recent study has shown similar incidence of pests on coffee grown in contiguous forest and forest fragments in this region of Ethiopia (Samnegård and Hambäck, 2014). Also of note is a higher proportion of granivores in forest than in shade coffee. This is an unusual result, as well, as granivores typically prefer disturbed and open habitats. Two granivorous species captured frequently in forest, Abyssinian Crimson-wing (*C. salvadorii*) and Green-backed Twinspot (*M. nitidula*), account for the greater relative abundance of granivores in forest. These two species were among the most commonly captured species in forest, accounting for 18% of all captures in this habitat. Unlike many other tropical studies (Şekercioglu, 2012a), shade coffee farms in our study did not have high numbers of open country granivores. This is an important result, as granivores can be agricultural pests. Frugivores were more common in shade coffee than in forest, a result that parallels pan-tropical findings (Şekercioglu, 2012a). An increase in frugivores in shade coffee is perhaps the result of selective thinning of the forest in favor of fruiting trees, a frequent practice in agroforests that helps to increase economic production.

These results indicate an important difference in overall community composition from specialists in forest to generalists in shade coffee. These findings are consistent with previous research (Komar, 2006; Şekercioglu, 2012a). Generalists are more widespread, relatively common, and less threatened than forest specialists (Şekercioglu, 2012a). Thus, while the high species rich-

ness in shade coffee is an encouraging result, the lower relative abundance of forest specialist species in shade coffee is illustrative of the importance of little-disturbed forest for many species.

4.3. Caveats

Mist netting is regarded as likely the best technique for assessing the relative abundance of tropical understory birds because it can detect species that are cryptic and/or less vocal and is repeatable with few observer biases (Karr, 1982; Newmark, 1991). Nonetheless, there are limitations and potential biases associated with mist netting data (Remsen and Good, 1996). For example, habitat modifications, such as removal of canopy trees and clearing of the understory may alter flight height of species, thereby changing their susceptibility to mist-net capture without changing their relative abundance (Arcilla et al., 2015; Remsen and Good, 1996). We recognize that the number of captures by species is therefore a result, at least in part, of how susceptible a species is to be caught by mist nets and of the habitat structure where the nets are placed. We have therefore made extensive efforts in this study to control for these potential biases. Accordingly, we restricted our analysis by removing species that do not consistently frequent the understory, and species that are not reliably caught in mist nets due to their large size, such as raptors, owls, and ravens (Wang and Finch, 2002). It should therefore be stressed that our results are restricted to interpreting differences in the understory bird community—not the entire bird community—between these habitats. While there was considerable difference in the structure between our shade coffee and forest sites, the average canopy tree height at our sites did not differ (Hundera et al., 2013). We also recognize that the three-year time period of our study could affect the relative abundance estimates of long-lived versus short-lived species. However, in one of the most rigorous studies of tropical forest bird longevity, results from Korfanta et al. (2012) show that the average life span of forest species in Tanzania's Usambara Mountains is 11.8 years. Taking this into account, we believe that a 3-year study period is relatively short compared to the average longevity of tropical forest species. Furthermore, longevity is positively related to body mass in most terrestrial organisms, including birds (Jones et al., 2003; Laurance, 1991), and we have excluded species of large body size from the analysis, which should help minimize any bias in this regard. Lastly, we believe that audio-visually obtained data, such as from point counts (e.g. Aerts et al., 2008), would substantially add to our understanding of bird community composition in Afromontane forest and shade coffee sites. Accordingly, a multi-year point count study is currently being conducted to improve our understanding of the bird communities in these habitats.

4.4. Agroforests and conservation

While shade coffee provides important habitat for many bird species, particularly those migrating from temperate regions, it is substantially different from forests and likely does not provide suitable habitat for all forest species. As evidenced in our study sites by the work of Hundera et al. (2013), shade coffee farming practices often involve the clearing of much of the diverse understory and mid-story of saplings, shrubs, and forbs, as well as the selective removal of large canopy trees. Native tree species are often replaced with those of greater economic value, including fruit and timber producers. Importantly, not all agroforests are created equally, and different farming practices can have profound impacts on biodiversity. For example, agroforests with higher percent shade cover and greater shade tree diversity have been shown to host a greater richness and diversity of birds (Clough et al., 2009a). Retaining shade cover and shade tree diversity on coffee farms may help preserve forest specialist birds, as well as insectivores and nectarivores, which can in turn benefit crop production

(Johnson et al., 2010; Maas et al., 2009; Şekercioğlu, 2012a; Şekercioğlu et al., in press). Further research on bird communities on coffee farms with different structural and floral components is needed to evaluate how these factors may impact bird communities.

Shade coffee farms may not provide viable habitat for all species found therein. Rather, some species may use these farms as stepping-stones between forest patches. Research globally has shown that “suboptimal” forest habitats, such as agroforests, secondary forest, plantations, and even individual trees can help increase connectivity of forest patches in agricultural landscapes (Berens et al., 2008; Ferraz et al., 2012; Neuschulz et al., 2011; Uezu et al., 2008). Research in northern Ethiopia demonstrated that forest restoration sites with suboptimal habitat can help connect forest fragments and also provide suitable habitat for some forest species (Aerts et al., 2008). Similarly, shade coffee farms in southwestern Ethiopia may help connect populations of species that rely on forests for breeding. Thus, the location of shade coffee farms may be important in determining their ecological value as links between forest patches.

4.5. Climate change threats

Climate change is predicted to have profound impacts on biodiversity (Thomas et al., 2004). It may cause as many as 900 bird extinctions over the next century, with the vast majority expected to occur in the tropics (Şekercioğlu et al., 2012). Tropical montane forest birds are among the most threatened of all bird species from climate change (Wormworth and Şekercioğlu, 2011) because they are often sedentary and have small ranges. Our study took place in and near Ethiopia's montane forests, which have a large number of endemic and range-restricted bird species that are expected to experience further range contractions with climate change. The distributions of montane birds in East Africa are predicted to shrink and become more isolated as arid areas expand in the region (Huntley et al., 2006). Human-induced habitat loss is likely to further exacerbate the effects of climate change on forest birds by reducing viable habitat and creating barriers to dispersal (Şekercioğlu et al., 2008). In order to preserve forest birds in Ethiopia—and forest biodiversity in general—reserves should incorporate wide elevational distributions and have high connectivity (Noss, 2001; Şekercioğlu et al., 2012). Shade coffee farms that are strategically located near forest patches may help improve connectivity of forests and help mitigate predicted extinctions. Furthermore, trees help buffer against climate change impacts, by improving water quality, reducing topsoil erosion, and creating microclimates (Bonan, 2008; Şekercioğlu, 2010). Encouragingly, there is evidence that Ethiopian farmers recognize these benefits, and are already working to mitigate the effects of climate change on crops by planting trees (Deressa et al., 2009).

Coffee production is also expected to suffer worldwide as a result of climate change. A global model estimates land suitable for growing coffee will decrease by about 50% by 2050 (Bunn et al., 2014). Interestingly, Ethiopia is one of the few locations where the suitability for coffee production is expected to improve. This model shows suitable land for coffee growing in Ethiopia shifting upwards with climate change, from rugged hillsides to the extensive highland plateaus. This scenario presents Ethiopia with a unique opportunity: by investing in shade coffee farming now, it may position itself to control a larger share of the lucrative coffee market in the future, while helping to mitigate the local effects of climate change by planting trees, and simultaneously benefiting the country's rich biodiversity by increasing connectivity of native forests. However, in order to conserve biodiversity,

it is also imperative to preserve remaining forest patches with minimal human disturbance.

4.6. Avian ecosystem services and “Shade Grown Coffee” certification

Approximately half of the global human population relies on subsistence or small-scale farming (Donald, 2004). Therefore, changes in ecological processes and ecosystem services can have profound impacts on human livelihood and well-being (Şekercioğlu, 2010). With a per-capita GDP of \$374 USD in 2011 (World Bank, 2012b), Ethiopia is one of the most impoverished nations on Earth. However, it has tremendous opportunities for sustainable development based on its high biological diversity, abundant natural resources, and potential for ecotourism. Shade coffee farming with high canopy cover and shade tree diversity have the potential to benefit not only the local ecology and biodiversity, but also the economy.

Birds provide valuable ecosystem services in agricultural areas, including pollination, predation of pests, seed dispersal, and ecosystem engineering (Şekercioğlu, 2006a, 2006b; Wenny et al., 2011; Şekercioğlu et al., in press). In the Neotropics, birds have been shown to provide economically valuable services to coffee farmers in the form of pest control (Clough et al., 2009b; Dietsch et al., 2007; Greenberg et al., 2000a, 2000b; Johnson et al., 2010; Perfecto et al., 2004; Şekercioğlu, 2006a, 2006b; Van Bael et al., 2008). For example, a study in Jamaica concluded that pest reduction by birds economically benefited coffee farmers by \$310 USD per hectare (Johnson et al., 2010). Investigating avian usage of and pest-regulating services in African shade coffee farms is a high priority, in order to compare with extensive findings from other regions of the world (Komar, 2006). Our results show that shade coffee farms in southwestern Ethiopia harbor a diverse and abundant insectivorous bird community. This is an important finding with implications for pest regulation on shade coffee farms. Fifteen coffee insect pests have been documented in the vicinity of our study, including the coffee berry borer (*Hypothenemus hampei*) and Coffee Berry Moth (*Prophantis smaragdina*), which can drastically damage coffee crops (Abedeta et al., 2014). Indeed, average Coffee Berry Moth incidence on coffee berries in the region was documented at 24.5%, with peak incidence of over 60% in some seasons (Mendesil and Tesfaye, 2009). Coffee berry borer is similarly ubiquitous in the region (Mendesil, 2004). This high prevalence of coffee pests implies that there may be large benefits from avian insectivory on shade coffee farms in Ethiopia. One study within the region documented similar pest infestation rates between shade coffee grown in contiguous forest and forest patches (Samnegård and Hambäck, 2014), but there is need for further investigation of the frequency of pest infestation and avian pest regulation in differing habitats where coffee is grown.

To our knowledge, our study documents the only known location in the world where all forest understory bird species recorded in primary forest control sites were also recorded in shade coffee sites (e.g. Wunderle and Latta, 1996; Tejada-Cruz and Sutherland, 2004; Philpott et al., 2008; Waltert et al., 2005; Aguilar-Ortiz, 1982). This is not altogether surprising, because coffee is native to our study region, whereas most studies of bird communities on coffee farms have occurred in the Neotropics, where coffee is an exotic crop. However, there is almost no awareness of this in the global “biodiversity friendly” coffee market. Certifying, publicizing and marketing Ethiopian coffee as “organic” “shade-grown” and “bird friendly” has the potential to increase incomes of local coffee farmers and provide them a major financial incentive to maintain traditional shade coffee farms instead of converting them into sun coffee plantations that are poor for biodiversity conservation. Farms in Ethiopia that have “shade grown” certification may receive as much as 15–20% more revenue per unit of crop

(Takahashi and Todo, 2013). Furthermore, shade coffee is widely regarded to be of superior quality to sun coffee, and is thus more valuable. These factors should be a significant consideration for local farmers in developing countries attempting to maximize profits (Philpott and Dietsch, 2003).

5. Conclusions

In studies around the world, shade coffee has been shown to support high bird species richness, albeit with fewer forest specialist species, particularly understory insectivores. Our results corroborate these findings. Shade coffee farms in southwestern Ethiopia had over double the species richness of nearby primary forest, while there was a much higher relative abundance of forest specialists, understory insectivores and Afrotropical-resident understory insectivores in primary forest. These groups are among the most extinction-prone birds globally. There were also some results that contrast with most global findings: (i) there was no difference in the relative abundance of all insectivores between the two habitats, and (ii) there was a greater relative abundance of granivores in primary forest. Our results support the consensus that shade coffee farms are an important habitat for forest bird conservation in the tropics. However, differences in the relative abundance of species in shade coffee and forest habitats indicate that intact forest must also be conserved in order to mitigate declines in forest specialist birds. Conserving all types of forested habitat is increasingly important for biodiversity conservation in the tropics (Gibson et al., 2011; Hernandez et al., 2013).

Humans can benefit in turn from conservation of forests and bird communities. Shade coffee farmers can profit from valuable ecosystem services provided by forest bird communities, such as pollination and insect regulation. These benefits can be economically significant, and may help contribute to poverty alleviation in Ethiopia—one of the most impoverished countries in the world. Shade coffee farms located near forest and those that maintain high levels of canopy cover and native tree diversity are particularly likely to benefit from avian ecosystem services. Our results imply that Ethiopian shade coffee is among the most “bird friendly” in the world. By promoting, certifying, and marketing shade coffee, Ethiopia has the potential to substantially increase revenue, while simultaneously helping conserve biodiversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.01.011>.

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