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Movement Ecology of Philippine Birds of Prey

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Movement ecology of Philippine birds of prey

Camille B. Concepcion

Dissertation submitted to the Davis College of Agriculture, Natural Resources and Design at West Virginia University

in partial fulfillment of the requirements for the degree of

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ABSTRACT

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Movement ecology is an emerging paradigm important to conservation biology and to the protection of global biodiversity. I used two common, but poorly known Philippine birds of prey as study tools in understanding movement ecology. One species is the migratory grey-faced buzzard (*Butastur indicus*), a raptor that which visits the islands in large numbers in winter. The other is the resident Philippine serpent eagle (*Spilornis holospilus*) which lives there at relatively high population density year-round. I used migration data at two terrestrial hawkwatch sites to assess how weather correlates influenced the movement behaviors of grey-faced buzzards. The grey-faced buzzard was the second most common raptor migrant using the Philippines as part of their migration route. My models show that they are more likely observed, either initiating or completing over-water crossings, in headwinds. I also created spatial models to understand how grey-faced buzzards overcome movement barriers (i.e. ocean). Modeled buzzard routes across the Philippines were between 1,582 and 2,970 km, and all repeatedly crossed water. Some of the routes overlapped at long and unavoidable over-water crossings. My models suggest that the optimal strategy for these birds is to find the shortest route to an exit point with the greatest possible access to stopover habitats and fewest over-water crossings under wind resistance. Additionally, I used road survey data to determine habitat associations of Philippine serpent eagle abundance across central and eastern Mindanao. My model showed that detection probability for the Philippine serpent eagle is relatively low, and the probability of occupancy was highest in near-pristine forests, especially low elevation dipterocarp forests. My road surveys helped establish the beginning of the breeding season for the Philippine serpent eagle. They also provided initial information on wintering habitats for grey-faced buzzards. This work is cutting-edge ecology and also

provided natural history information about species for which there is almost no existing knowledge.

DEDICATION

For my Lolo (grandpa) Fred -

As usual, you were right.
This is more amazing than flying airplanes.

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Like the song says, "*ang kinabuhi ko o Dios, Kanimo lamang.*"

TABLE OF CONTENTS

CHAPTER 1: LIST OF FIGURES

CHAPTER 2: LIST OF TABLES

CHAPTER 2: LIST OF FIGURES

CHAPTER 3: LIST OF TABLES

CHAPTER 3: LIST OF FIGURES

CHAPTER 4: LIST OF TABLES

CHAPTER 4: LIST OF FIGURES

CHAPTER 5: LIST OF TABLES

CHAPTER 5: LIST OF FIGURES

CHAPTER 5: LIST OF APPENDICES

CHAPTER 1

Introduction

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RATIONALE

The Philippines is one of the most speciose and most threatened of global biodiversity hotspots (Myers et al. 2000, Hannah et al. 2013). However, the archipelago has experienced, and continues to experience, high rates of deforestation, estimates of which range from 217 km^2 to 2000 km^2 of forest loss annually (Lasco and Pulhin 2000, Bankoff 2007). The problem is so severe that today, only 3% of the Philippines' original 275,000 km^2 primary forest remains (Myers et al. 2000, Bankoff 2007). If secondary forests are included, total forest cover is estimated at 12% (Catibog-Sinha and Heaney 2006). Consequently, the country is recognized as a priority area for reducing decline in agricultural productivity and biodiversity loss under projected climate change (Myers et al. 2000, Hannah et al. 2013).

Understanding the impacts of this habitat fragmentation and loss on Philippine biodiversity is essential to conserving populations of the species that remain. To do this, it is crucial to understand how movement of individuals interacts with demography to impact animal ecology and response to habitat change (Nathan 2008).

For example, habitat fragmentation can drive spatial and temporal changes in avian populations by affecting territory size and dispersal (Rolstad 1991). Raptors may be relatively more impacted by habitat change than other birds because they occur at relatively low densities and have relatively large home ranges, and because they are often persecuted by humans.

The Philippines has 29 diurnal birds of prey species (Kennedy et al. 2000). With the exception of work on the endemic and critically endangered Philippine eagle (*Pithecophage jefferyi*; Gonzales 1968, Kennedy 1981, Salvador and Ibanez 2006) and a few other birds of prey, the vast majority of these species have gone largely unstudied.

The Philippine eagle is a useful umbrella for conservation because survival of its population continues to be threatened by habitat loss, decline in prey abundance, demographic instability and threat of disease (BirdLife International 2001). These threats are mostly driven by human actions and are not necessarily independent of each other. Conservation of this iconic species depends on better understanding of the processes and conditions that have supported its continued existence. For example, although it is known that juveniles will spend more time at the forest edge than the adults, the effects of frequent movement outside the forest borders on juvenile dispersal and survival is yet to be established (Afan et al. 2000).

As a rare species of great cultural importance, the Philippine eagle is quite difficult to study because there are so few individuals left, encounter rates are low and there are massive legal and logistical hurdles to its study. If information is needed about this and other endemic Philippine raptors, it would make more sense to focus on common species and draw inferences about them that could then be applied to harder to study species. With this in mind, this study focused on two common but poorly researched Philippine raptors as a mechanism to understand movement ecology of Philippine raptors in a heavily fragmented tropical ecosystem. These are the migratory, winter resident grey-faced buzzard (*Butastur indicus*) and the non-migratory, year-round resident Philippine serpent eagle (*Spilornis holospilus*).

I studied two common species because (a) common species should occur in larger numbers than rare species, ensuring a good sample size and greater statistical power; (b) by studying two species with different ecologies, I can more fully understand how habitat change impacts the suite of local raptors; and (c) the rarity and legal protection of the highly-endangered species creates logistical hurdles that make research on those taxa nearly impossible. Thus, these two common species are intended to serve as both indicators of general trends in biodiversity in the Philippines and also proxies for less common but ecologically similar taxa.

I will adopt the conceptual framework for movement ecology defined by Nathan et al. (2008). Movement ecology is a paradigm that provides common context and tools towards a “better understanding of the causes, mechanisms, patterns, and consequences of all movement phenomena” (Nathan 2008). This framework is based on three basic components that characterize the study individuals (internal state, motion capacity and navigation capacity) and a fourth basic component related to external factors that affect movement.

The internal state accounts for the physiological conditions that provides the motivation (goal) for an individual to move. Motivations for movement may include factors as variable as seeking a safe place to spend winter, reproduce and establish a territory. The ability of an individual to move to fulfill these goals is referred to as motion capacity, while the ability to orient movement in time or space are related to navigation capacity.

Movement may occur at different spatiotemporal scales – “movement step,” “movement phase,” or “lifetime track” (Nathan et al. 2008). A movement step is a displacement from one location to another. A movement phase, on the other hand, is a sequence of steps and stops associated with fulfilling a particular goal. A complete sequence of steps and stops from birth to death is a lifetime track.

Understanding the movement behavior of an individual is important to understand spatial population dynamics (Patterson et al. 2008, Schick et al. 2008). Movement behavior also relates to how individuals mix and interact with the population and community (Morales et al. 2010) and is influenced by body condition. These in turn impact fitness, vital rates, energy balance, and food provisioning. Further, movement of individuals shape biodiversity by providing links between habitats or ecosystems and by facilitating coexistence in communities (Jeltsch et al. 2013).

The use of extrinsic or intrinsic markers is a common approach in studying movement ecology. Extrinsic markers involve the use of telemetry or individual tags which are both direct ways of monitoring movement (Kendall and Nichols 2004). Telemetry, for example, has allowed researchers to gather vast amounts of data on animal positions that together are used to establish movement phases (Cagnacci et al. 2010). These data have also been used to relate movement to external factors such as landscape properties (Bennetts and Kitchens 2000, Cagnacci et al. 2010) and meteorological conditions (Mandel et al. 2008, Sunde et al. 2014). Intrinsic markers, on the other hand, can either be biological (e.g. morphological and behavioral) or biogeochemical (e.g. trace element concentrations and stable isotopes) (Rubenstein and Hobson 2004). For example, stable isotope analysis has been used to establish foraging preferences and migration connectivity for birds (Inger and Bearhop 2008). Results from stable isotope analysis could be enhanced by combining it with other markers, such as bird banding or telemetry (Van Wilgenburg and Hobson 2011).

FOCAL SPECIES

The **grey-faced buzzard** is a migratory bird of prey that breeds in eastern mainland Asia and winters in Southern China and parts of Pacific Asia (Ferguson-Lees and Christie 2001). It regularly engages in over-water travel during migration and is considered one of the most oceanic of raptor migrants (Bildstein 2006). Every year, more than 10,000 grey-faced buzzards migrate through Taiwan before crossing 180 kilometers of open ocean to reach the Philippines (Lin and Severinghaus 1998). Grey-faced buzzards exhibit high fidelity to both migration route and to stopover sites (Shiu et al. 2006) and the species' passage is a good indicator to identify important watchsites (Lin and Severinghaus 1998).

The grey-faced buzzard is said to occupy open habitat and typically hunts outside the forest (Gamauf et al. 1998, Sakai et al. 2011). It favors foraging in wet open areas, most commonly cultivated rice paddy fields, where it hunts prey such as frogs, lizards and grasshoppers (Matsuura et al. 2005, Wu et al. 2006, Kadowaki et al. 2007). The rice fields more often used share edges with forests or wooded areas. These are also the characteristic of the preferred migration stop-over sites, and wintering and breeding habitats (Matsuura et al. 2005, Ueta et al. 2006, Wu et al. 2006, Sakai et al. 2011). The loss of these habitats through the abandonment of traditional rice paddy fields has led to the well-documented rapid decline in grey-faced buzzard breeding population in Japan (Kawakami and Higuchi 2003, Ueta et al. 2006).

The **Philippine serpent eagle** is a common resident of the Philippines which is endemic to the main islands of the archipelago (Ferguson-Lees and Christie 2001). There currently are poor data to support any accurate population estimate for this species, but it is believed that there are about 10,000 breeding individuals in the country. Movements of these birds are almost completely unknown and it is in fact, one of the least known raptors in the world (Meyburg 1986, Ferguson-Lees and Christie 2001).

The Philippine serpent eagle occupies habitat with over 50% canopy cover and hunts above the forest (Gamauf et al. 1998). Although primarily found in forests, it may also occupy "edge" habitats, wooded foothills and open country with scattered trees (Ferguson-Lees and Christie 2001). Foraging ecology of the Philippine serpent eagle is believed to be comparable with crested serpent eagle sub-species, preying mostly on reptiles, small mammals, and birds.

OBJECTIVES

My research objective was to link movement behavior to seasonal movement and distribution. Understanding this link will help predict how disturbance and habitat change may alter biodiversity and ecology in these heavily fragmented tropical ecosystems.

The main questions my research answered were:

1. How do external factors shape movement behavior?
2. How does the inherent capacities of the species to move influence the "movement phase" when confronted with ecological barriers?

3. How does the individual internal state direct movement steps and associated behavior?

Studying two species of birds of prey whose movement ecology differs allowed me to evaluate comprehensively their conservation status as well as the impacts of human disturbance and land-use change on these two important components of the Philippine raptor community.

To address my first research question, I specifically aimed (1) to quantify external factors (e.g., weather) that influence grey-faced buzzard migratory performance; and (2) to identify landcover characteristics that render areas suitable as Philippine serpent eagle territory.

To address my second research question, I built spatial models to predict grey-faced buzzard migration routes and bottlenecks across the Philippines.

To address my third research question, I presented notes on Philippine serpent eagle breeding behavior as well as grey-faced buzzard wintering distribution.

METHODS

Study area

My research took me to different islands of the Philippines. I made the remote town of Basco in the province of Batanes, and Cape San Agustin in the province of Davao Oriental as the center of my grey-faced buzzard research (Figure 1). Basco is at the northernmost tip of the country, perfect for monitoring the passage of birds using the East-Asian Oceanic Flyway as they cross 180 km of ocean from Taiwan to the Philippines. Cape San Agustin is at the southeastern tip of the island of Mindanao, allowing for monitoring of migrant birds as they cross 170 km of ocean to presumed destinations in Indonesia.

I targeted five sites in the south of the country, on the island of Mindanao, for studying the resident Philippine serpent eagle (Figure 1). These areas were identified according to their varying habitats (in terms of forest type, disturbance and elevation), as follows:

- Lantapan, Bukidnon (a near-pristine, high elevation montane forest);
- Arakan, North Cotabato (a severely disturbed, high elevation montane forest);
- Davao City (a moderately disturbed, high elevation montane forest) ;
- San Isidro, Davao Oriental (a near-pristine, low elevation Dipterocarp forest); and
- Governor Generoso, Davao Oriental (a moderately disturbed low elevation Dipterocarp forest)

These areas belong to different biogeographic regions, but their land cover is broadly representative of the Philippines as a whole. In the north, in Batanes, habitats are coastal areas and lowland old-growth and secondary evergreen forests. The island is dominated by hills and mountains and peaks at around 1,000 meters above sea level. The province experiences subtropical, Type II climate, with no dry season and a marked rainy season peak from December to February (DOST-PAGASA 2004).

Mindanao habitat ranges from lowland rainforests to high elevation montane forests. Lowland rainforests has been highly degraded by logging. The highest point on the island of Mindanao reaches 2,954 meters. The study sites range from coastal hills to inland mountain ranges. Mindanao has mostly Type IV tropical climate with rainfall more or less evenly distributed through the year (DOST-PAGASA 2004).

Data collection

Question 1. How do external factors shape movement behavior?

I answered this question by assessing how the grey-faced buzzard's migratory movement phase was influenced by external factors. A migratory movement phase for the grey-faced buzzard is a sequence of steps and stops in seeking a safe place to spend winter. External factors expected to influence movement phases of Philippine birds of prey are landscape properties and meteorological agents. Landscape properties were defined by combining land cover and land use information.

I used the established technique of monitoring the visible migration of birds at migration watchsites to study how the grey-faced buzzard used the Philippine landscape. My project was the first to use full-season, bird of prey migration monitoring in autumn in the Philippines. Movement data collected via direct observation was then connected to datasets on weather (wind speed and direction are critical to ocean crossings by most species) and on land-use.

Counts at a single watchsite occurred from August through November, during daylight hours from 0600 to 1700h, as weather permitted (Bildstein et al. 2007). I stopped data collection in the event of strong rains or typhoon. Locations and directions of flight were determined using a GPS and compass.

I spotted migrating raptors by methodically using binoculars, field scopes and the unaided eye to scan the sky in the direction the migrants were expected. Single individuals or flocks were followed until identified and, for each group of birds, I recorded the time, counted the number and established the species and direction of travel. I recorded migration and weather data on datasheets I patterned after the Hawk Migration Association of North America. Weather data were logged hourly and recorded using a handheld anemometer or weather station.

I used migration data to assess how weather influenced the grey-faced buzzard's movement phase. The decision to migrate, and to cross open ocean, were then statistically correlated to weather conditions that the birds encounter. This allowed me to predict expected migration flights given a set of weather conditions as I establish and assess other hawkwatches in the future.

Similarly, I answered this question by assessing how the Philippine serpent eagle's movement phases are influenced by the Philippine landscape. A movement phase of an adult serpent eagle is a sequence of steps and stops in seeking either a safe place to reproduce or, in the case of immatures, a safe place to establish a territory for immature birds. To understand distribution and habitat associations, I successively visited each of the five study sites at the beginning of the breeding season (November) and conducted time constrained surveys. With the aid of binoculars, I conducted road transects to census for bird abundance, counting from a vehicle at an approximate speed between 25 to 40 km/h (Andersen et al. 1985, Viñuela 1997). I covered 10 km in each site, looping through habitat types (forests and open areas). For one of my survey years, I supplemented this with surveys from fixed observation posts located on ridge tops, cleared hills and near logging roads that would offer a vantage of the forest and forest edges. Locations of the road transects and observation posts were determined using a GPS. I recorded observations on datasheet I patterned after the Hawk Migration Association of North America.

I used population survey and mark-resight analysis to estimate occupancy and detection. I linked these with movement behavior based on habitat associations.

Question 2: How does the inherent capacities of the species to move influence the "movement phase" when confronted with ecological barriers?

I established how the ocean, an important ecological barrier, influenced movement phases by studying the grey-faced buzzard, one of the world's most oceanic raptor migrants. As previously mentioned, to reach the Philippines, the grey-faced buzzard crosses the Bashi Channel, a 180-km stretch of the Pacific Ocean found between Taiwan and the Philippines.

Ecological barriers considered in this study are not necessarily complete barriers to movement. Instead, I define them as landscape features that penalize movement duration and/or incur an additional risk of mortality once crossed (Bélisle and St. Clair 2001, Alerstam 2001).

The ocean has largely been thought of as a physical and ecology barrier to movement that causes detours in migration routes and carries an added energy cost (Alerstam 2011). However, recent studies of ocean raptor migration suggest that the ocean may instead be an ecological corridor (López-López et al. 2010) that is shaped by the flexible response of migrants to wind and ocean currents (Klaassen et al. 2011, Mellone et al. 2011).

I created spatially explicit models to compare how the grey-faced buzzard's movement varies in response to environmental parameters. I started by establishing the spatial temporal distribution of wind variables that provide better support for grey-faced buzzard motion capacities. I also established potential movement stops. Based on this, I built spatially explicit models comparing cost distances to address how movement phases were adjusted according to the ocean as a barrier.

Question 3: How does the individual internal state direct movement steps and associated behavior?

One internal state is finding a safe place to spend winter. I used my population surveys to present some initial observations regarding the winter distribution of grey-faced buzzards around central and eastern Mindanao.

Another internal state is establishing a new territory and reproduction. I similarly used my population surveys, to present natural history information for the Philippine serpent eagles.

LIMITATIONS OF THE STUDY

Most of my results are based on data collected using direct observation. For this reason, most of my research on grey-faced buzzards are on the visible migration of raptors. I was also only able to do single season migration counts for each of my watchsites. These counts were completed in different years. My observations though, remain particularly important because so few over-water crossings have been studied outside of Europe.

I was able to establish a fruitful relationship with indigenous trappers, experienced in capturing grey-faced buzzards. However, the birds we got in hand had compromised wings, and were not fit for telemetry. This prevented me from testing hypotheses from my spatial models.

Further, all my attempts at capturing Philippine serpent eagles failed. Despite this, I conducted three years of road surveys along the same transects. This provided me with good quality data that was useful for answering one of my research questions. The road surveys were also useful in helping build natural history information for the Philippine serpent eagle.

NATURAL HISTORY INFORMATION

As mentioned, there have been few attempts at studying birds of prey in the Philippines. Even basic natural history information is lacking for most of these species. For example, it was my road surveys that established the beginning of the breeding season for Philippine serpent eagles (question # 3). I first observed Philippine serpent eagles in courtship display in October of 2014. The following year, in November, I observed a pair in mutual flight, with one adult carrying nesting material. This information is new to science. Unfortunately, I had limited field time and was not able to find an active Philippine serpent eagle nest.

Road surveys were also useful for gathering initial information on wintering habitats for grey-faced buzzards (questions # 3). I found grey-faced buzzards to occupy a wide range of habitats, both open areas and forests, and near-pristine to severely disturbed landcover. Grey-faced buzzards were also found in both low elevation and high elevation forests. Unfortunately, I did not have enough observations of grey-faced buzzards to estimate either wintering survival or occupancy correlates.

CONTENTS OF THE DISSERTATION

My dissertation comprises five chapters. This first chapter provides a brief introduction to the study, goals and objectives, research approach and limitations. It also provides notes from observations in the field that do not completely answer any of my research questions but are relevant towards answering them in the future with further investigation.

Chapter 2 provides the context for studying birds of prey in the Philippines by examining the conservation threats and status of birds of prey found in Asia first. In this chapter, I describe how birds of prey in Asia are faring relative than birds of prey elsewhere in the world. I identified the Philippines as one of the most speciose countries and one of the countries that has the most threatened species.

In Chapter 3, I use hawk migration data to assess how external factors (i.e. weather correlates) influence the movement behaviors of grey-faced buzzards (question # 1). I first described the overall patterns of migration as hawks complete and begin their oceanic crossings in the Philippines. I then compared migration behavior of grey-faced buzzards with migration behavior of *Accipiters*. These two species were the most common migrants observed using the East Asian Oceanic Flyway.

In Chapter 4, I used road survey data to determine habitat associations of Philippine serpent eagle distribution across central and eastern Mindanao (question #1). I put my findings in context by looking at raptor abundance, and comparing the correlates of Philippines serpent eagle distribution (habitat specialist) with the correlates of distribution of a habitat generalist.

Finally, in Chapter 5, I created spatial models to understand how grey-faced buzzards overcome movement barriers (question # 2). I created models to explain the optimal migration strategy of hypothetical grey-faced buzzards as they repeatedly face the decision of completing, delaying, or foregoing over-water travel.

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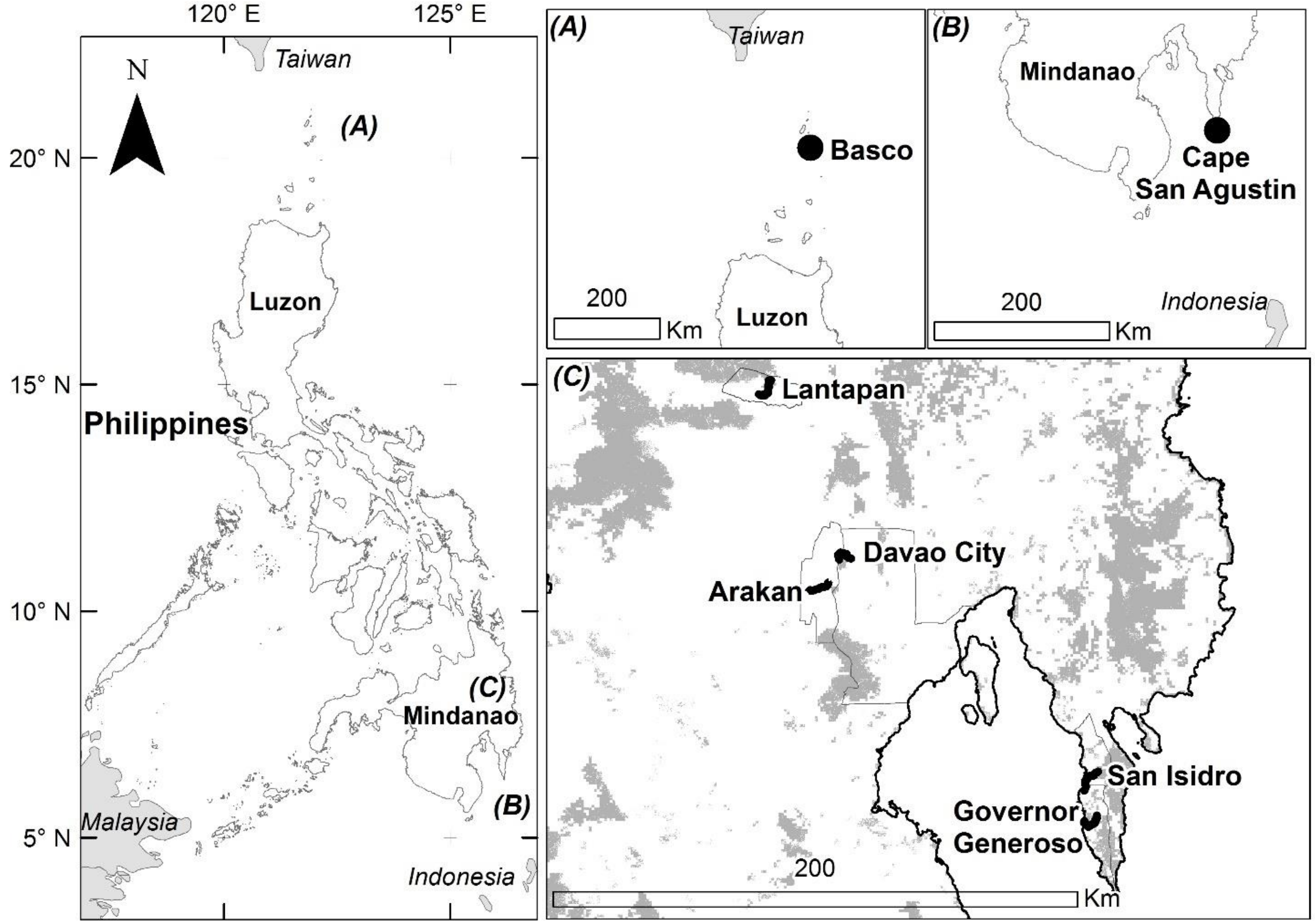

Figure 1. Geographic locations of study areas around the Philippines. Left inset shows the entire Philippines. Figure part (A) shows the location of the watchsite (●) at Basco and part of Taiwan, which is 180 km north, and mainland Luzon of the Philippines, 280 km south. Top right map (B) shows the location of the watchsite (●) at Cape San Agustin found in the island

of Mindanao, as well as the northernmost islands of Indonesia (Sulawesi), 170 km south. Bottom inset (C) shows the distribution of areas where 10-km road transects (━) where surveyed. Areas shaded grey in c have at least 50% tree cover and are from Bartholomé and Belward (2005) and Hansen et al (2013). Outlines in c show town boundaries of study sites.

CHAPTER 2

Conservation threats and priorities for raptors across Asia

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ABSTRACT

Asia is the largest and most populous continent in the world and features one of the world's greatest assemblages of raptors. Here, we summarize Asian raptor diversity, along with the threats that many of these species face across their annual lifecycle, and identify key conservation priorities. Asia has 105 species of hawks, eagles and vultures, 22 falcon species and 108 owl species. Of these, 81 are globally Threatened and Near-Threatened; with 8 listed as Critically Endangered, 11 as Endangered, and 22 as Vulnerable, and 40 as Near-Threatened. Among 150 non-threatened raptor species, populations of 39% are decreasing. Agriculture and aquaculture, biological resource extraction and pollution are the most significant threats. Forests and anthropogenic terrestrial areas are most commonly occupied by Asian raptors and are the most used land-use types for Threatened and Near-Threatened species. Within the continent, south and southeast Asia have comparatively greater raptor diversity and the highest endemism than do any other continental region. Eight of the ten countries that have the greatest number of Threatened and Near-Threatened species are found in south and southeast Asia. Our review of the literature indicates that raptors in Asia are relatively more at risk than elsewhere in the world.

INTRODUCTION

With long coastlines and some of the world's most important rivers, mountain ranges, high-altitude plateaus, and islands, Asia is the largest and most populous continent in the world (Lyde 1904, Spencer 1954, Population Reference Bureau 2016). Asia supports all major terrestrial ecosystems and all major climatic types (Galloway et al. 1998, Braimoh and Huang 2015). These include barren icefields and taigas in north Asia, boreal forests and cold deserts in west, central and east Asia, temperate and tropical forests (wet and dry) in east and southeast Asia, and grasslands in central and south Asia (Udvardy 1975, Braimoh and Huang 2015). Together, the ecoregions of Asia foster some of the greatest biodiversity on Earth, including six (24%) of 25 global biodiversity hotspots (Myers et al. 2000).

With 47% of the world's Threatened and Near-Threatened raptor species (Table 1), Asia is home to 42% of the world's diurnal and nocturnal raptor species, including 30% of all migratory species, and 51% of all endemic species. With the exception of work on raptors in tropical Asia (i.e. southeast Asia; Thiollay 1985, 1998, Bildstein 1998), the *Gyps* vultures of south Asia (Prakash et al. 2003, 2012, Gilbert et al. 2004, Shultz et al. 2004, Acharya et al. 2009, Hall et al. 2011, 2015) and a few other country-level studies, the population status of the vast majority of these species has gone largely unstudied. The raptors of south and southeast Asia provide a useful umbrella for conservation because the survival of their populations continue to be threatened by land-use change, direct human persecution and environmental contaminants (Bildstein 1998, Thiollay 1998). These threats rarely act in isolation and are directly or indirectly caused by human activities. Raptors are especially vulnerable to these threats because of their life history traits, and because they occur at relatively low population densities and in relatively large home ranges (Newton 1979, 1998, Real and Mañosa 1997, Hall et al. 2015).

Threats to Asian raptors

Of the threats that Asia's raptors face, land-use change is most significant. Agriculture has modified natural landscapes more than any other human activity and among the most rapidly expanding agricultural industries are oil palm *Elaeis guineensis* and rubber *Hevea brasiliensis* (Clay 2004). The conversion of natural landscapes greatly reduces species richness and diversity (Aratrakorn et al. 2006, Beukema et al. 2007, Fitzherbert et al. 2008, Sodhi et al. 2010). Loss of raptor habitats can also drive spatial and temporal changes in avian populations by affecting territory size and dispersal (Rolstad 1991).

Land-use change also can carry over to loss of habitat of prey species and the consequent reduction in prey abundance. Declines in prey abundance could result in decreases in nesting density and reproductive success of predatory avian populations (Andersson 1978, Newton 1980, Terraube et al. 2011). Decline in prey abundance also can cause conflict with humans if domestic animals are taken as alternative prey (Carrete et al. 2007).

Land-use change magnifies the threat of human persecution as encounters with people increase in fragmented and human-impacted landscapes. Humans have long intentionally destroyed nests, and shot and poisoned raptors they consider as pests (Newton 1979, 1998, Bildstein 2001). Human persecution has resulted in raptor population declines by reducing reproductive rates and pre-adult and adult survival (Whitfield et al. 2004a, 2004b, Tenan et al. 2012), and has caused range retractions and local extinctions of raptor populations (Newton 1998, Smart et al. 2010).

Environmental contaminants and secondary poisoning also severely impact Asian raptor populations (Newton 1979, 1998, Sheffield 1997, Oaks et al. 2004a, Shultz et al. 2004). Pesticides (Ratcliffe 1970, Mineau et al. 1999, Jagannath et al. 2008), and heavy metals (Solonen and Lodenius 1984, Wallin 1984, Lourenço et al. 2011) are known to reduce survivorship or impair raptor reproductive success. Anticoagulant rodenticides (Stone et al. 2003, Lambert et al. 2007), pharmaceuticals (Oaks et al. 2004a), and lead (Kramer and Redig 1997, Fisher et al. 2006, Gangoso et al. 2009) can weaken or directly kill individuals.

Below we summarize raptor diversity in mainland and oceanic Asia. We then describe the threats that many of these species face, and identify priority species and essential steps for their conservation. We close with a section on poorly known species in Asia and opportunities to fill knowledge gaps that will benefit conservation of raptors in this immense but poorly studied continent.

METHODS

We define Asia as the area that includes Asiatic Russia in the north, Indonesia in the south (including West Papua, although the avifauna of New Guinea is predominantly Australasian) and from Japan in the east to Uzbekistan, Turkmenistan, Afghanistan and Pakistan in the west (Figure 1). Although the Middle East is, geographically, part of Asia, its avifauna is composed predominantly of European and African species, and we do not consider this area in our treatment of Asian raptors.

Distributions, conservation statuses, threats, raptor habitat and taxonomy were based on BirdLife International (BirldLife International 2017). BirdLife International provides the most extensive data on the world's bird species and has been compiling data on threatened bird species since 1966. They are the designated Red List Authority for birds (IUCN 2017). BirdLife regularly assess species at a global level and update their database based on published information and data collected by 120 partner organizations worldwide (one partner for each country). BirdLife provided us with a database of Asian raptor species including information on Red list category, migratory status, and current population trend. The database also includes country of occurrence and land cover types occupied (13 categories). Threats (11 classifications) to globally threatened and near-threatened species are also available.

We summarize the overall Asian raptor diversity and break down the information according to threats, regions, and countries. Regions are also based on BirdLife International (BirldLife International 2017). We look at overall population trends and population trends per land cover type, again using BirdLife International (2017) data. Subspecies are not differentiated in our summaries. We also consulted Ferguson-Lees and Christie (2001) for distribution and population trends but followed BirdLife's taxonomic convention.

RESULTS

Asia is home to 235 raptor species (Table 1). In total, Asia has 8 Critically Endangered raptor species (Table 2), 11 Endangered, 22 Vulnerable, and 40 Near-Threatened species, with a majority of species (64%) listed as Least Concern. Twenty-six percent of Asia's raptors are migratory and 31% are endemic to a single country (Table 1).

Of Asia's raptors, 105 are hawks, eagles and vultures (Accipitriformes), distributed among 30 genera (Table 1). Of these, 19% (n = 20) are globally Threatened and 13% (n = 13) are Near-Threatened. Forty percent of Asia's hawks, eagles and vultures are migratory, and 18% are endemic to a single country. The continent is home to 22 falcon species, in 3 genera. Of these, 5% (n = 1) are globally Threatened and 23% (n = 5) are Near-Threatened. Forty-five percent are migratory and 41% are endemic to a single country. Asia is also home to 108 owl species, in 14 genera. Of these, 19% (n = 20) are globally Threatened and 19% (n = 21) are Near-Threatened. About 7% are migratory and 48% are endemic to a single country.

Overall, Asia's raptors are faring slightly worse than average raptors elsewhere in the world (Table 1). A greater proportion of Asia's owls (19%) and migratory species (12%) are Threatened compared to similar species elsewhere in the world (owls: 18%, migratory species: 8%). There is also a greater proportion of Asia's owls (19%) and migratory species (8%) that are Near-Threatened compared to species elsewhere in the world (owls: 11%, migratory species: 6%). Additionally, a greater proportion of Asia's falcons (23%) and endemic species (31%) are Near-Threatened compared with falcons and endemic species elsewhere in the world (falcons: 14%, endemic species: 22%).

Of the threats to Asian raptors, agriculture and aquaculture (e.g. livestock, wood and non-timber crops, and freshwater and marine aquaculture) and biological resource extraction (logging, hunting) are thought to be the greatest threats to Asia's eagle, hawk, vulture and owl species (Table 3). Pollution and biological resource extraction are thought to be the greatest threats to Asian falcons. Secondary threats to these taxa include these same forces as well as changes to land cover, urbanization, and energy production.

Of Asia's 235 raptor species, populations of 57% (n = 133) are decreasing (Figure 2). This includes 97% (n = 33) of globally Threatened and Near-Threatened species of hawks, eagles and vultures, all 6 globally Threatened and Near-Threatened falcon species, and 88% (n = 36) of globally Threatened and Near-Threatened owl species. Among the 150 non-threatened raptor species, populations of 46% (n = 32) eagles, hawks and vultures, 31% (n = 5) of falcon species, and 33% (n = 21) of owl species are decreasing.

Among the 13 land-use types, forest, man-made or anthropogenic terrestrial (e.g. degraded forests, plantations, arable land, rural gardens and urban areas), shrubland, grassland and wetlands were the most commonly occupied by Asian raptors (Figure 3). Forests are most important for 86% (n = 202) of Asia's raptor species, and a disproportionately high number (36 of 41) of Asia's globally Threatened raptor species are found in forests. Additionally, although anthropogenic terrestrial land use appears to be acceptable habitat for Least Concern species, 44% (n = 18) of globally Threatened, and 54% (n =22) of Near-Threatened species are found here as well. Finally, 21% (n = 17) of globally Threatened and Near-Threatened species occupy shrubland, 20% (n = 16) occupy grassland, and 16% (n = 13) occupy wetlands.

At a sub-continental (regional) scale, north Asia (Figure 1) has 61 raptor species, 80% of which migrate (Table 4). Although the region has no endemic raptors, its ecosystems are important breeding areas for globally threatened species including Steller's Sea Eagle *Haliaeetus pelagicus* and Blakiston's Fish-owl *Bubo blakistoni*.

North Asia has no Critically Endangered species (Table 2), 4 Endangered, 4 Vulnerable, and 4 Near-Threatened species.

West and central Asia (Figure 1) have 59 raptor species, 75% of which migrate (Table 4). The region has no endemic raptors, but includes important areas for globally threatened and rare species, including Eastern Imperial Eagle *Aquila heliaca*, Steppe Eagle *Aquila nipalensis*, Red-footed Falcon *Falco vespertinus* and Saker Falcon *Falco cherrug*. West and central Asia has 2 Critically Endangered species (Table 2), 3 Endangered, 3 Vulnerable, and 7 Near-Threatened species.

East Asia (Figure 1) has 96 raptor species (Table 4). There are no endemic species in this region, and 59% of its raptors migrate. All of Asia's migratory owls are in east Asia. The region's notable raptors include Steppe Eagle, Pallas's Fish-eagle *Haliaeetus leucoryphus*, Saker Falcon and Amur Falcon *Falco amurensis*. East Asia has 2 Critically Endangered species (Table 2), 4 Endangered, 5 Vulnerable, and 7 Near-Threatened species.

South and southeast Asia has the greatest raptor diversity, with 219 species, only 20% of which migrate. Endemism is also highest in this region: 74 species are found only in Asia. South and southeast Asia also has the highest number of globally Threatened and Near-threatened species, including 8 Critically Endangered (Table 2), 10 Endangered, 21 Vulnerable and 39 Near-Threatened. Important species in this region include the critically threatened vultures of the Indian subcontinent, as well as two of the most evolutionarily distinct and globally threatened raptors in the world, the Forest Owlet and the Philippine Eagle.

We identified ten Asian countries that have the most Threatened and Near-Threatened species (Table 5). Among these countries, eight are in south and southeast Asia and the remaining are in north and east Asia. These ten countries have 231 of the 235 raptor species of Asia, including 72 of the 74 Asian endemics. Because of the inclusion of China, Russia and India, they also include the vast majority of the land mass of the continent. China, Russia and India also have the highest number of migratory species (51, 48 and 46 species, respectively).

Indonesia and the Philippines have the highest number of endemics – 39 and 23, respectively – 54% and 74% of which are globally Threatened and Near-Threatened. Additionally, Indonesia (29%) and the Philippines (38%) also have the highest proportion of globally Threatened and Near-Threatened species.

DISCUSSION

Overview

Our review indicates that Asia's raptors are faring slightly worse than average raptors elsewhere in the world. Asia's owls and migratory species are at greater risk than similar raptors elsewhere in the world. Additionally, more falcons and endemic species are close to qualifying for a threatened category in the near future than falcons or endemic species elsewhere in the world.

Perhaps not surprisingly, forest is the most frequently used land type and a vast majority of Threatened and Near-Threatened species are found here. What is surprising is that anthropogenic landscapes such as degraded forests and forest plantations appear to be the second most frequently used land type for Threatened and Near-Threatened species. Forests are also the most used by most of Asia's endemic species, and once again artificial landscapes, the second most important. Largely treeless ecosystems, like shrublands and grasslands, and inland wetlands are also frequently used by Asia's raptors. However, only a small proportion of Threatened and Near-Threatened species are found in each of these land cover types. Out of Asia's endemic species, only four endemic owls are found here.

In all likelihood, this does not mean that degraded forests or plantations, for example, are of equal quality to natural landscapes, such as forests. These anthropogenic land-use types may be used, but are still of low quality for reproduction or survival (Watson 1992, Donovan and Thompson 2001, Battin 2004, Carrete et al. 2009). It is therefore important for researchers and conservation practitioners to not just determine occupancy of individuals in different land cover types, but to evaluate population structure as well, in order to ascertain whether the use of these altered areas is a result of optimized selection or lack of choice (Van Horne 1983).

Threats

Agriculture and aquaculture, biological resource extraction, and pollution are the most common threats to Asia's raptors. Combined, the threats that raptors in Asia face can be grouped into indirect effects and two kinds of direct effects on raptor populations (threats that lead to unintentional fatalities and those that lead to targeted removal of individuals from a population).

Indirect effects

Indirect effects of land-use change and disturbance are the most significant threat to Asia's raptors. Raptors may be relatively more impacted by habitat change than other birds because they occur at relatively low densities, have relatively large home ranges, and because they are often persecuted by humans (Newton 1979, 1998). For example, land use change reduces available suitable space and might alter home range sizes (Andersson 1978). If degradation occurs on a large enough scale, it can reduce breeding densities by birds that are forced to occupy larger home ranges (Newton 1980, Amar et al. 2011). Fragmentation additionally creates movement barriers for individuals and affect the movement of individuals among suitable areas (Harrison and Emilio 1999, Bélisle and Desrochers 2002, Harris and Reed 2002).

The effects of land-use change are likely to grow as Asia's economy and infrastructure grows, and those effects are difficult to reverse, especially in tropical areas (Brooks et al. 2006). Agriculture, specifically, has been responsible for converting ~13 million hectares of previously untouched forests to croplands globally every year over the past 30 years (Clay 2004). Agriculture also remains the most widespread occupation for Asian people and agricultural production has been growing alongside industrial production (Galloway et al. 1998, The Association of Academies of Sciences in Asia 2011). Looking forward, it is estimated that between

2000 and 2050, 10 billion hectares of natural landscapes in the world will be converted to agriculture (Tilman et al. 2001).

In tropical Asia, for example, in the past 40 years oil palm plantations have expanded faster than any other type of food or industrial agricultural crop (Clay 2004). Malaysia and Indonesia currently have over half of the world's total oil palm plantation area. In these two countries, although pre-existing croplands were converted to oil palm plantations, over half of oil palm cultivated areas replaced native forests (Koh and Wilcove 2008). Further, between 1910 and 1940, rubber plantations in Indonesia increased ten-fold (Burger and Smit 2001). Seventy percent of all rubber tree plantations are currently in Malaysia, Indonesia and Thailand (Clay 2004). By the year 2024, the expansion of rubber plantations is expected to continue and it is estimated that 4.3 to 8.5 million hectares of forests and swidden land would be needed to answer the global rubber demand (Warren-Thomas et al. 2015).

The expansion of agriculture has also impacted natural grasslands. Grasslands are heavily used by certain raptor speciesand are one of the most endangered terrestrial ecosystems (Hoekstra et al. 2005). West and central Asia, in particular, is a global stronghold for natural grasslands (Hoekstra et al. 2005), and, as a result of the region's low densities of human populations, until the mid-1900s central Asian ecosystems were largely pristine (Zlotin 2002). However, steppe was targeted by the Virgin Lands project of the USSR and between 1953 and 1963 an estimated 23 to 25 million hectares of semi-desert grasslands were ploughed and converted to agriculture (Kamp et al. 2011, Kraemer et al. 2015) which has had negative consequences for raptor populations (BirdLife International 2001, Sánchez-Zapata et al. 2003).

Direct effects – Targeted removal of individuals

Consumptive uses of a few species, particularly falconry and the pet trade, are thought to drive trajectories of some raptor populations. For example, Saker Falcons are an Endangered species whose population has been reduced to a tenth of its former abundance (BirdLife International 2001, Kenward 2009). As many as 1,000 Saker individuals (~8% of global population) were estimated to have been taken illegally from west and central Asia, particularly Kazakhstan, between 1994 and 1996 (Levin 2011). Small numbers of Sakers have always been traded in west and central Asia, but illegal trading only flourished in 1992 after the fall of the Soviet Union. This geopolitical event opened west and central Asia's borders and increased foreign access to its Saker population (Kenward 2009). In east Asia, especially Mongolia, populations of the Endangered Saker Falcon are over-trapped (Fox 2001, Zahler et al. 2004). Between 1997 and 2010 alone, an average of 286 Saker Falcons were traded annually (Dixon et al. 2011). Unfortunately, although local policies are in place to protect Saker Falcons, it is often difficult to enforce those regulations.

Steppe Eagles, Imperial Eagles, and 27 other species, are also sold in markets in China (Yi-Ming et al. 2000, Zhang et al. 2008). Most are taken from the wild during migration (Kenward 2009). More recently, birds are being traded online in south and southeast Asia. In 2015 alone, over 7,500 individuals from 22 diurnal raptor species and 11 owl species were traded online in southeast Asia (Iqbal 2016).

There are also unique forms of consumptive uses in south and southeast Asia. In India, for example, owls are important in witchcraft and believed to bring gambling luck (Ahmed 2010, Jathar and Rahmani 2013). To answer the demand for witchcraft, between 1992 to 2008, >1,000 individuals of 15 species of owls were traded (Ahmed 2010). Another consumptive use occured in the Doyang Reservoir region of Nagaland, northwestern India, where the mass killing of Amur Falcons for human consumption was a major threat (Symes 2012, Dalvi and Haralu 2014). These long-distance migrants form large communal roosts while migrating. During peak migration, as many as 15,000 falcons were taken daily with mist nest, and 120,000—140,000 falcons were killed annually. Fortunately, since 2013, the killings of Amur Falcons have been halted as a result of education campaigns and continued population monitoring (NWBCT 2017).

Direct effects – Unintentional fatalities

The catastrophic collapse of the *Gyps* population in India is well documented, with an estimated 92% population decline between 1993 and 2000 (Prakash et al. 2003) and further declines since that time. As of 2012 only 0.1 – 3.2% of original populations remained (Prakash et al. 2012). Similar declines were also recorded for vulture populations in Nepal (Baral et al. 2004, Shultz et al. 2004) and in Pakistan (Gilbert et al. 2004, Oaks et al. 2004b). The decline of *Gyps* vulture was put into spotlight not just for its magnitude but also for the severe economic, cultural and human health effects that followed (Prakash et al. 2004, Markandya et al. 2008). This cataclysmic phenomenon was attributed to contamination of carcasses with the veterinary drug, Diclofenac, that causes vultures to develop visceral gout and acute kidney failure leading to death (Oaks et al. 2004a, 2004b).

In 2006, following the identification of the role of Diclofenac, India consequently banned the drug from veterinary use (Taggart et al. 2007). Nepal and Pakistan declared similar bans in 2006, and in 2010 while Bangladesh followed in 2010 (Prakash et al. 2012). This ban and the promotion of the Diclofenac-alternative, Meloxicam (Swarup et al. 2007, Pain et al. 2008), has lowered, but not eliminated, the Diclofenac's impact (Prakash et al. 2012, Cuthbert et al. 2014, 2016, Galligan et al. 2014). Captive care and breeding of Indian vultures, with a goal of eventual release into the wild, is also currently ongoing (Prakash et al. 2004, Markandya et al. 2008). Vulture restaurants providing clean food likewise are a strategy used to reduce the impacts of Diclofenac (Gilbert et al. 2007).

Migratory species may also encounter environmental contaminants in their stopover and wintering areas. For example, Lake Baikal basin, a large steppe area, once had the highest known north Asian concentration of Eastern Imperial Eagles (Ryabtsev and Katzner 2007, Ryabtsev 2011). The population here has declined by at least 80% in the past few decades possibly due to fatalities caused by environmental contaminants in tropical wintering grounds in southeast Asia (Ueta and Ryabtsev 2001, Ryabtsev and Katzner 2007). Unfortunately, the extent and effects of environmental contaminants are not well studied in the tropics (Lacher and Goldstein 1997). However, this is a highly plausible cause of population decline given the potential environmental impacts of intensified agriculture in southeast Asian countries (Tinker 1997, Mineau and Whiteside 2013). Another example is the threat of contaminants to Steller's Sea Eagles that breed on Sakhalin Island and winter in Japan. In summer, Steller's Sea Eagles typically feed on fish. However, during harsh winters or during periods of overfishing, these birds shift feeding habits and scavenge on sika deer *Cervus nippon* (Shiraki 2001). This has led to increasing incidences of lead poisoning, when birds feed on hunter-killed, but unrecovered, deer or offal (Urosawa 2000, Saito 2009).

Finally, Asia's long-distance migratory species also may face pressures outside of Asia. For example, Pallid Harriers *Circus macrourus* and Red-footed Falcons *Falco vespertinus* breed in central Asia and their populations are complete migrants (Galushin et al. 2003, Panuccio 2007, Brochet et al. 2016, Katzner et al. 2016). On migration, far from their breeding or wintering grounds, these species pass through geographic bottlenecks in Europe where shooting birds of prey is common.

Priority species

Asia holds a third of the world's Critically Endangered raptors, including two of the most genetically distinct birds of prey, the Philippine Eagle and the Forest Owlet (Jetz et al. 2014). These species, along with the Endangered *Gyps* species, are endemic to the Asian continent and have undergone drastic population declines making them among the highest regional priorities for conservation (BirdLife International 2001).

The Philippine Eagle, whose wild population is estimated at 82 to 250 pairs (Bueser et al. 2003, BirldLife International 2017), is emblematic of Asia's raptor conservation problems. The species is endemic to the Philippine archipelago (Kennedy 1981, Kennedy et al. 2000) and occupies Philippine tropical forests (Bueser et al. 2001), of which only 3% now remains (Myers et al. 2000). Beyond land-use change, it faces threats from shooting, trade, electrocution, and environmental contaminants. Extensive deforestation also reduced space for the

Philippine Eagle's prey base (Kennedy 1985, Concepcion et al. 2006) and has increased opportunities for human persecution. Although the Philippine Eagle receives legislative protection (Salvador and Ibanez 2006), its current estimated population decline remains at 2 — 10% per year (Ibañez et al. 2016).

Globally, no other continent has a higher proportion of migratory raptor species than Asia (Bildstein 2006). Forty percent of all migratory raptors of Asia are endemic to the Asian continent; these endemics include Pallas's Fish-eagle, Steller's Sea Eagle and the Himalayan Griffon. Although a majority of Asia's most threatened raptors are not migratory, 15% are full migrants. Migratory raptors of Asia are also faring considerably worse than average migratory raptors elsewhere. Further, compared to their European and African counterparts, Asian populations of cross-continental migrant species are largely unstudied (Kirby et al. 2008). As an example, migrants using Asia's Oceanic and Continental Flyways are poorly known and only recently have studies been published on this flyway (Concepcion et al. *in press*, Bildstein 2006). All of these factors make Asia's migratory raptors high priority for conservation and research.

Migratory species face unique threats in their breeding, stopover and wintering habitats (Webster et al. 2002). For such species, especially species with large home ranges, creation of protected areas for breeding sites alone often is not an efficient conservation approach (BirdLife International 2001, Finch et al. 2017). Comprehensive and actionable management plans would allow identification of these unique threats across all these habitats and provide a framework for addressing those threats.

Priority regions and countries

Among regions, south and southeast Asia have the highest number of species overall, the highest number of endemic species, and the highest number of globally Threatened and Near-Threatened species. Sixty-two percent of Threatened species and 56% of Near-Threatened are island endemics. As a result, raptors of south and southeast Asia are more at risk than elsewhere in the continent. Eight of the 10 most speciose Asian countries that also have the most Threatened and Near-Threatened species are also found in this region. This diversity of raptors can be partly attributed to the extent of tropical forests that once covered most of the region (Olson and Dinerstein 2002, Laurance 2007). Unfortunately, tropical forests are extremely vulnerable landscapes (Brooks et al. 2006) and those in southeast Asia have experienced, and continue to experience, higher rates of conversion than elsewhere in the world (Laurance 1999, Sodhi et al. 2004). This is to the detriment of south and southeast Asia's raptors that heavily use these forests.

There is a significant lack of information for tropical Asia's raptors, especially of island endemics (Thiollay 1985, McGowan et al. 1998, BirdLife International 2001). With the exception of work on a few charismatic species such as the Philippine Eagle and the Javan Hawk-eagle, most of the region's raptors continue to be largely unstudied. South and southeast Asia is a conservation and research priority region. Protection of the region's raptor species, especially of island endemics, intrinsically has a disproportionately large impact on the global raptor population. There is therefore a need to collect ecologically sound information to enable their protection.

Priority topics for research

Without basic information on species biology and demography, it can be difficult to properly direct conservation and management strategies for raptors (Collar 1997, Van Balen et al. 2000, BirdLife International 2001, Mace and Collar 2002, Sutherland et al. 2004, Katzner et al. 2011). For example, Pallas's Fish-eagle is probably the world's most poorly studied Northern Hemisphere eagle (Katzner and Tingay 2010). It is classified as Vulnerable on the basis of reported population declines (BirdLife International 2001, Ferguson-Lees and Christie 2005). Although its precise distribution is poorly known, the main breeding populations of Pallas's Fish-eagle are thought to be in China, Mongolia and India (Ferguson-Lees and Christie 2005, BirldLife International 2017), with lower-density populations in surrounding countries. However, recent field work suggests that Mongolia never was a breeding stronghold for the species (Gilbert et al. 2014), the implication being that conservation action directed there may have little impact for this species. This finding illustrates how a lack of knowledge can confound potential conservation programs.

Apart from research on species biology and demography, there are other overlapping research needs for Asia's Threatened and Near-Threatened species (BirdLife International 2001). There is also a need to identify specific threats to populations and reasons for population declines. For migratory species, this extends to describing the different pressures faced in summer, migratory and wintering areas (Webster et al. 2002). Likewise, there is a need to study biology, demography and threats of prey species on which raptors depend (BirdLife International 2001). Finally, laboratory studies may also be important to identify disease and the physiological effects of environmental contaminants (Lacher and Goldstein 1997, BirdLife International 2001).

The effects to raptors of renewable energy and electrocution are also priority topics for research, especially in Asian grassland and treeless ecosystems. As energy development has rapidly grown in west and central Asia, electrocution has become a growing concern for raptor populations (Kamp et al. 2016). Separate surveys in Kazakhstan documented that as many as 21 raptor species died from electrocution, including eight threatened and near-threatened species such as the Saker Falcon, the Egyptian Vulture *Neophron percnopterus* and the Steppe Eagle (Karyakin 2008, Lasch et al. 2010, Levin and Kurkin 2013, Pestov et al. 2015). In east Asia, particularly in Mongolia, older, wood pole electrical structures are being replaced with concrete poles with grounded metal crossarms. The energized parts of these newer, concrete poles are closer to the ground than the older wood poles, which in turn have increased electrocution of raptors (Harness et al. 2008). As many as 13 species, including 4 migrants, have been documented dying from electrocution in this region (Dixon et al. 2013).

Research elsewhere suggests that new threats may emerge from development of wind and solar energy. Collision with wind turbine blades, for example, can cause trauma or death (Madders and Whitfield 2006, Smith and Dwyer 2016). Trauma and death could also come from solar tower facilities as a result of collision with infrastructure or exposure to concentrated solar energy or solar flux (Smith and Dwyer 2016, Walston et al. 2016). There also are threats of collision, disturbance and land use change even before these facilities are completed (Tsoutsos et al. 2005, Smith and Dwyer 2016). Wind energy is particularly interesting because its direct and indirect effects on raptor populations can alter demography (Katzner et al. 2013).

Poorly known species

Poorly known species are an important priority for research. Four out of six (67%) of the world's Data Deficient raptor species occur in Asia (Table 1; BirdLife International 2017). These are the Chestnut-shouldered Goshawk *Erythrotriorchis buergersi*, Papuan Boobook *Uroglax dimorpha*, Seram Masked Owl *Tyto almae*, and the Nicobar Scops-Owl *Otus alius* of south and southeast Asia. All three owls are island endemics.

Modern and updated identification literature is also key to the quality and reliability of ecological studies (BirdLife International 2001). Establishing identification literature is made more challenging because some Asian species are only now being recognized (eg. *Spizaetus philippinesis* complex: Gamauf et al. 2005, *Ninox philippensis* complex: Rasmussen et al. 2012). Accurate identification of species is obviously crucial to conservation as unrecognized species may be lost due to lack of protection (Gamauf et al. 2005). This is of particular concern in south and southeast Asia where the range of landscapes available, the isolation of some of these landscapes, and the geography of the region (i.e. islands of varying sizes and distances to the mainland) contribute to a high level of endemism (Gentry 1992, White and Kiff 2000).

CONCLUSIONS

Raptors are more at risk in Asia than elsewhere in the world. Our summary of Asia's raptor diversity and human threats supports the need to continue cataloguing the status, threats and needs, and understanding conservation priorities for these species. Holding almost half of all the world's raptor species, and half of all the endemic species, the continued decline and potential loss of raptors in this region is truly a global concern.

One of the things highlighted in our summary is the lack of information on Asia's raptor species. This lack of information is exemplified in the scarce literature available for raptors of Asia. For example, compared to raptors of other tropical regions, tropical Asia has the least published information (Kiff et al. 2007). There also are instances when information is available but unavailable in international abstracting services or unavailable in English (Kiff et al. 2007, Clavero 2010). Similarly, researchers in Asia may have limited access to published information or limited opportunities to publish in English journals (Salager-Meyer 2008).

Lack of information may also mean that actions will not be taken until some species are lost. For example, data from long-term migration monitoring informed of the population decline of several species in North America due to organochlorides (Bednarz et al. 1990). The relatively early-warning provided ample time to determine the cause of decline and to respond appropriately (eg. Bald Eagle: Grier 1982, Fraser et al. 1996, Watts et al. 2008). This and other types of monitoring are lacking for most, if not all, of Asian species.

Conservation urgency presents opportunities for future work. The establishment of the Asian Raptor Research Network (ARRCN) in 1998 has created a community for researchers of Asian raptors (Kiff et al. 2007). The ARRCN is vital in sharing valuable information through organizing symposia, promoting communication among researchers and disseminating published abstracts. With access to training, mentoring and funding, it is possible for current and rising raptor researchers in Asia to begin systematically addressing threats and knowledge gaps. Like most things in these contemporary times, international collaboration would be vital in achieving these goals.

Simply put, much work remains to be done to elevate conservation efforts in the continent to at least those of elsewhere in the world. The time to start is now, before many common species decline to the status of conservation priority, and before less common species become extinct.

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Table 1. Distribution and conservation status of raptors in the world and in Asia based on BirdLife International (2017). Migratory species include species with a significant portion of populations that make seasonal, cyclical and predictable movements. Endemic species are species that breed in a single country.

	Accipitriformes		*Falconiformes*		*Strigiformes*	
	World	*Asia*	*World*	*Asia*	*World*	*Asia*
Total	251	105	66	22	241	108
Migratory	165	42	15	10	17	8
Endemic	52	20	8	2	86	52
Extinct	1	0	2	0	5	0
Critically Endangered	14	6	0	0	7	2
Endangered	14	5	2	1	9	5
Vulnerable	25	9	4	0	27	13
Near Threatened	33	14	9	5	27	21
Least Concern	163	70	49	16	161	64
Data Deficient	1	1	0	0	5	3

Table 2. Asia's Critically Endangered (CR) and Endangered (EN) raptor species based on BirdLife International (2017). Migratory species include species with a significant portion of populations that make seasonal, cyclical and predictable movements. Endemic species are species that breed in a single country.

					Asian Region			
Species	*Common Name*	*Category*	*Migratory*	*Endemic*	*North*	*West & Central*	*East*	*South & Southeast*
Accipitriformes								
Aquila nipalensis	Steppe Eagle	EN	Y	N	x	x	x	x
Gyps bengalensis	White-rumped Vulture	CR	N	N			x	x
Gyps indicus	Indian Vulture	CR	N	N				x
Gyps tenuirostris	Slender-billed Vulture	CR	N	N				x
Neophron percnopterus	Egyptian Vulture	EN	Y	N				x
Nisaetus bartelsi	Javan Hawk-eagle	EN	N	Y				x
Nisaetus floris	Flores Hawk-eagle	CR	N	Y				x
Nisaetus philippensis	North Philippine Hawk-eagle	EN	N	Y				x
Nisaetus pinskeri	South Philippine Hawk-eagle	EN	N	Y				x
Pithecophaga jefferyi	Philippine Eagle	CR	N	Y				x
Sarcogyps calvus	Red-headed Vulture	CR	N	N			x	x
Falconiformes								
Falco cherrug	Saker Falcon	EN	Y	N	x	x	x	x
Strigiformes								
Bubo blakistoni	Blakiston's Fish-owl	EN	N	N	x		x	
Heteroglaux blewitti	Forest Owlet	CR	N	Y				x

					Asian Region			
						West &		South &
Species	*Common Name*	*Category*	*Migratory*	*Endemic*	*North*	*Central*	*East*	*Southeast*
Ninox leventisi	Camiguin Boobook	EN	N	Y				x
Ninox rumseyi	Cebu Boobook	EN	N	Y				x
Otus alfredi	Flores Scops-owl	EN	N	Y				x
Otus siaoensis	Siau Scops-owl	CR	N	Y				x
Otus thilohoffmanni	Serendib Scops-owl	EN	N	Y				x

Table 3. Summary of ongoing threats to globally Threatened and Near-Threatened diurnal and nocturnal raptor species of Asia. Threats are based on BirdLife International (2017). Percentages represent proportions of Threatened and Near-Threatened species in Asia.

	Accipitriformes	*Falconiformes*	*Strigiformes*
Agriculture and aquaculture	27 (79%)	2 (33%)	39 (95%)
Biological resource extraction	29 (85%)	5 (83%)	39 (95%)
Climate change and severe weather	3 (9%)	0	0
Energy production and mining	8 (24%)	0	11 (27%)
Human intrusions and disturbance	4 (12%)	0	1 (2%)
Invasive and other problematic species, genes and diseases	10 (29%)	0	1 (2%)
Natural system modifications	11 (32%)	2 (33%)	12 (29%)
Pollution	16 (47%)	4 (67%)	0
Residential & commercial development	7 (21%)	2 (33%)	15 (5%)
Transportation & service corridors	7 (21%)	0	4 (37%)
Total number of species	34	6	41

Table 4. Summary of distribution and conservation status of raptors in according to regions of Asia based on BirdLife International (2017). Migratory species include species with a significant portion of populations that make seasonal, cyclical and predictable movements. Endemic species are species that breed in a single country. Percentages indicate proportion of Threatened and Near-Threatened migratory and endemic species.

	North Asia	*West and Central Asia*	*East Asia*	*South and Southeast Asia*
Total	61	59	96	219
Migratory	49 (20%)	44 (25%)	52 (21%)	51 (20%)
Endemic	0	0	0	74 (64%)
Critically Endangered	0	2	2	8
Endangered	4	3	4	10
Vulnerable	4	3	5	21
Near Threatened	4	7	7	39
Least Concern	49	44	78	137
Data Deficient	0	0	0	4

Table 5. Summary of distribution and conservation status of raptors in ten Asian countries with the most Threatened and Near-Threatened raptor species based on BirdLife International (2017). Migratory species include species with a significant portion of populations that make seasonal, cyclical and predictable movements. Endemic species are species that breed in a single country. Percentages indicate proportion of Threatened and Near-Threatened migratory and endemic species.

	Indonesia	India	Russian Federation	Philippines	Myanmar
Total	133	102	102	55	88
Migratory	24 (4%)	46 (22%)	48 (21%)	14 (0%)	39 (21%)
Endemic	39 (54%)	9 (67%)	0	23 (74%)	0
Critically Endangered	3	5	0	1	3
Endangered	3	3	6	4	2
Vulnerable	12	5	7	6	6
Near Threatened	20	13	8	10	8
Least Concern	92	75	81	34	69
Data Deficient	3	1	0	0	0

	Nepal	Bangladesh	Malaysia	China	Thailand
Total	83	77	67	94	76
Migratory	39 (26%)	33 (27%)	28 (21%)	51 (22%)	32 (19%)
Endemic	0	0	1 (100%)	0	0
Critically Endangered	3	3	3	2	3
Endangered	3	3	1	4	1
Vulnerable	4	4	5	4	5

	Nepal	Bangladesh	Malaysia	China	Thailand
Near Threatened	9	8	8	6	6
Least Concern	64	59	50	78	61
Data Deficient	0	0	0	0	0

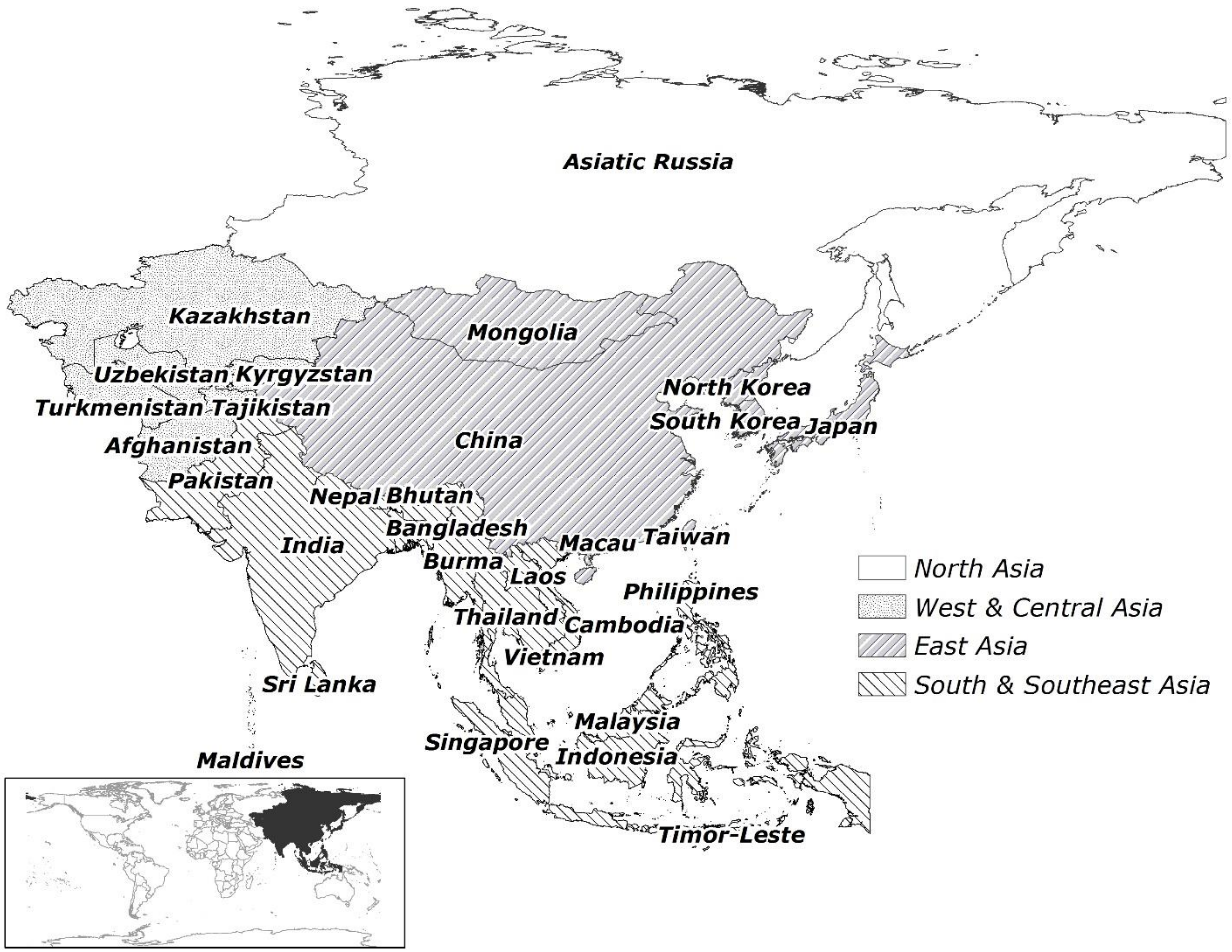

Figure 1. Regional Asia. Country boundaries are from the Global Administrative Areas database (www.dabm.org) and, in some regions (e.g., borders of India with Pakistan and China), are not fixed owing to on-going territorial disputes (Fravel 2015). The Middle East is not included.

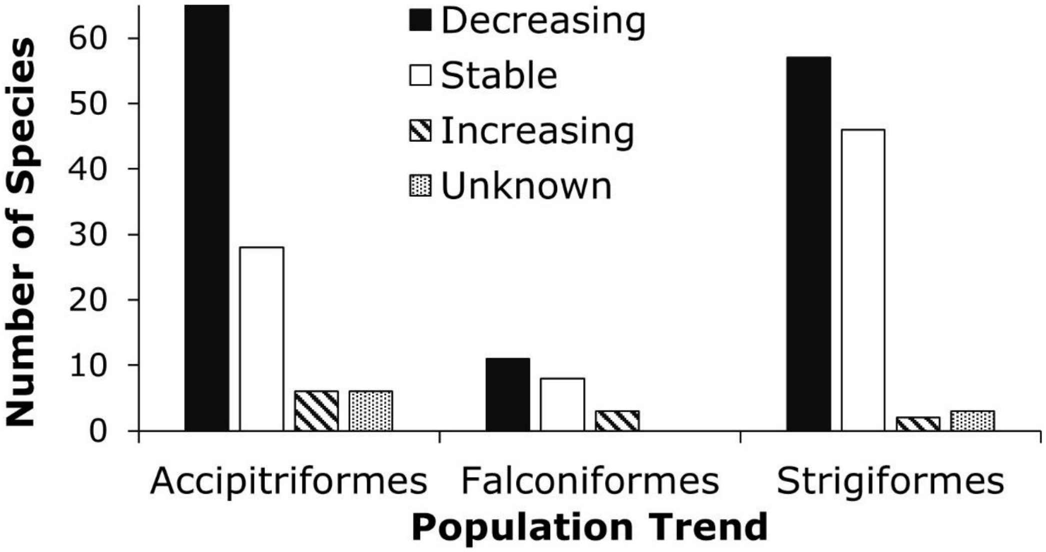

Figure 2. Population trends of Asian raptors. Population trends are based on BirdLife International (2017). Population trend is either directly estimated or suspected based on existing threats and other factors. Population estimates were not taken in the same year and global population sizes have been estimated between 1999 to 2016.

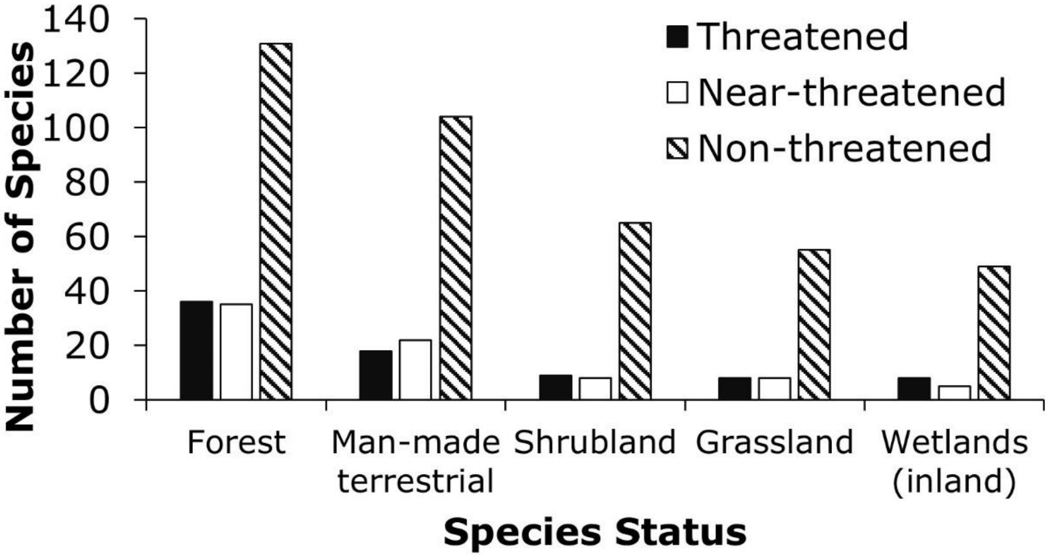

Figure 3. Species status of Asian raptors found in the five most occupied land types. Conservation status and land types are based on BirdLife International (2017).

CHAPTER 3

Species composition, timing, and weather correlates of autumn open-water crossings by raptors migrating along the East-Asian Oceanic Flyway

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ABSTRACT. --Raptor migration rarely involves long-distance movements across open oceans. One exception occurs along the East-Asian Oceanic Flyway. We collected migration data at two terrestrial hawkwatch sites along this flyway to better understand open-ocean movements along this largely overwater corridor. At the northern end of the Philippines, at Basco on the island of Batan, we recorded 7587 migratory raptors in autumn 2014. Near the southern end of the Philippines, at Cape San Agustin on the island of Mindanao, we recorded 27,399 raptors migrating in autumn 2012. Chinese Sparrowhawks (*Accipiter soloensis*) were the most common species observed, making up approximately 89% and 92% of total records for Basco and Cape San Agustin, respectively. The Grey-faced Buzzard (*Butastur indicus*) was the second most common raptor migrant, accounting for 8% of the total counts at both watch sites. The migration period was about 1–2 wk earlier at Basco, the more northerly site, than at Cape San Agustin. Overwater flights at Basco peaked in both the morning and late afternoon, whereas at Cape San Agustin there was only a morning peak. In general, the rate of migration passage at both sites was highest with clear skies when winds were blowing from the northwest. However, we observed interspecific differences in migration behavior at both sites, with *Accipiters* more likely to be observed with tailwinds and eastward winds and Grey-faced Buzzards more likely observed with headwinds. These results help to characterize poorly known aspects of raptor biology and to identify potential migratory bottlenecks or key sites for raptor conservation in little-studied Philippine tropical ecosystems.

KEY WORDS: *Chinese Sparrowhawk*; Accipiter soloensis; *Grey-faced Buzzard*; Butastur indicus; *East-Asian Oceanic Flyway*; *migration*; *overwater crossing*; *Philippines*

Understanding animal movement is central to conservation planning and ecological knowledge (Nathan 2008). For migratory birds, determining patterns of migratory connectivity and identifying flyway bottlenecks are important parts of interpreting animal movement. For raptors, counts at migration watchsites globally have documented these patterns, especially over land (Bildstein 2006). Oceanic crossings by raptors are less well studied, but they do have important effects of funneling populations (Meyer et al. 2000, 2003, Panuccio et al. 2005), limiting demography (Germi et al. 2009, Panuccio et al. 2012, Oppel et al. 2015) and affecting ecology (Kerlinger 1985, Panuccio et al. 2005, Bildstein 2006, López-López et al. 2010).

In spite of the potential negative consequences of ocean crossings for raptors, recent studies indicate that for some species, oceans also may be significant ecological corridors (López-López et al. 2010), the forms of which are shaped by the flexible response of migrants to predominant wind and water currents (Klaassen et al. 2011, Mellone et al. 2011). In some cases, overwater crossings may even have benefits for raptors. In particular, they can provide both shorter and more direct routes to destinations (Meyer et al. 2003), and they can offer the potential to avoid unfavorable weather conditions (Yamaguchi et al. 2011), pathogens, and parasites (Gill et al. 2009). However, environmental correlates of oceanic crossings are generally poorly understood, making it difficult to identify why some birds may choose to cross the open ocean.

The East-Asian Oceanic Flyway is the world’s most heavily travelled oceanic raptor migration corridor (Bildstein 2006). Birds traveling this route use seasonal monsoon winds, trade winds, and sea thermals (*sensu* Augstein 1980) to complete their migration. During autumn, raptors leave southern Taiwan and cross at least 180 km of ocean to reach the northernmost islands of the Philippines. Most of these birds then island-hop across the Philippines, with some wintering in-country and others continuing their journeys further south. Those that continue south often depart from the southern Philippine island of Mindanao to presumed destinations in Indonesia that are at least 170 km away (Fig. 1).

We conducted exploratory migration research along the East-Asian Oceanic Flyway to quantify the magnitudes of the flights along this corridor. We then used these data to assess correlates of migration behavior as a basis for an initial attempt at understanding the factors associated with ocean crossings. We focused our effort on birds entering and exiting the Philippine archipelago, between Taiwan and Luzon in the north and between Mindanao and the Sulawesi archipelago of Indonesia in the south (Fig. 1). We used data collected during two full-season counts (one count for each of two sites) to evaluate four questions about raptor migration into and out of the Philippines: (1) when, during the migration season and during the day, do oceanic crossings occur?; (2) in what directions do observed migrants fly?; (3) what are the weather conditions under which birds initiate and complete oceanic crossings?; and (4) are there among-species differences in timing and meteorological correlates of oceanic crossings along this route? We interpret these findings in the context of hypotheses describing the potential value of the oceanic crossings birds make and the evolutionary forces that may shape these behavioral patterns.

METHODS

Study Areas. We counted migrating hawks at a northern entry point to the Philippines (Basco) and a southern exit from the archipelago (Cape San Agustin). Basco is on Batan Island, at the northernmost tip of the Philippines (Fig. 1). The island belongs to a small archipelago located between the Bashi Channel, south of Taiwan, and the Balintang Channel north of Luzon Island. Grasslands dominate the local ground cover. Batan has subtropical climate, with average monthly temperatures of 22–28°C. Rainfall averages 2.8 m annually and is uniformly distributed among months. Cool winds are characteristic, especially during December, January and February, when the northeasterly trade winds pass through the islands.

Cape San Agustin on the island of Mindanao separates the Celebes Sea to the east from the Davao Gulf to the west (Fig. 1). Land cover in the region includes natural forest, primarily mangrove (*Rhizopora* spp.), along the intertidal zone, and coconut (*Cocos nucifera*) plantations and farmlands in the coastal plain and upland hillsides. The climate of the peninsula is greatly influenced by monsoonal and trade winds. From June to October a monsoonal wind blows from the southwest. Starting in November, that southwest monsoon transitions into a northeast monsoon. The average monthly temperature is 22–33°C with little seasonal variation. Average rainfall is about 1.2 m annually.

We conducted counts from locations with good views on both islands. At Basco this was the 20-m-tall Naidi Lighthouse (20°27’5”N 121°57’51”E). The lighthouse has a panoramic view of the northern part of Batan Island, as well as of parts of several islands directly adjacent to Batan Island. We conducted the count at Cape San Agustin approximately 2 km north of the tip of the peninsula (6°16’47”N 126°11’30”E). The count site was a 4.5-m-tall bamboo tower we built in a coconut plantation. Despite the elevated post, coconut trees partially obstructed our view to the south.

Survey Techniques. Counts at Basco were conducted by two or three observers (CBC, PTD, and MRS) working together between 25 August and 19 October 2014. The period during which we conducted counts was based on reported dates of departure of Grey-faced Buzzards (*Butastur indicus*) and Chinese Sparrowhawks (*Accipiter soloensis*) from southern Taiwan (Lin and Severinghaus 1998). Counts at Cape San Agustin were conducted by one observer (CBC) between 12 September and 30 October 2012. Timing of this count was estimated based on known arrivals of birds for the Indonesian island of Sangihe 280 km to the south (Germi et al. 2009).

We recorded migration and weather data hourly on a daily data sheet derived from a template produced by the Hawk Migration Association of North America (see Bildstein et al. 2007). We counted migrating raptors according to standardized migration watchsite count protocols (Bildstein et al. 2007). We conducted observations from 0530 H to 1730 H (Basco) and from 0600 H to 1530 H (Cape San Agustin). We methodically scanned the horizon using binoculars (10×) and unaided eyes to ensure consistent coverage, and visually tracked single individuals or flocks until we identified them and were able to determine their direction of travel. We classified flight direction as either expected flight direction (i.e., passage on a northern to southern axis) or unexpected flight direction (i.e., passage on a southern to northern axis or to a west to east axis). We classified altitude of flight as either low (i.e. below eye level to about 30 meters above ground) or high (i.e. more than 30 meters above ground). We counted most passing migrants individually but, in instances of large flocks (>100 individuals) or when the birds had already passed us, we counted birds in groups of 2, 5 or 10. If the birds were first spotted soaring in groups, we waited until we could count them individually or as groups streamed north-to-south across the count site. To ensure accuracy, we repeated and averaged counts of groups whenever possible, especially when flocks were larger than 100.

We measured temperature and wind speed at Basco using a Kestrel 4000 Weather Meter (The Nielsen-Kellerman Company, Birmingham, MI 48009 USA) and at Cape San Agustin using an Anemometer HT816 (Long Term Inc., Ningbo Shi, Zhejiang Sheng 315000, China). Wind speed was recorded in m/s and converted into U and V components using the following equations (Wallace and Hobbs 2006):

$$U\ Component = -wind\ speed * \sin\left(wind\ direction * \frac{\pi}{180}\right)$$

$$V\ Component = -wind\ speed * \cos\left(wind\ direction\ * \frac{\pi}{180}\right)$$

We used a compass to determine wind direction (i.e., N, SE, NE) and converted estimates into azimuth degrees for these equations, for example where south wind was 180° and west wind was 270°. We estimated cloud cover as the percent of sky with background cloud cover.

Data Analysis. We used a paired Wilcoxon signed-rank test to compare within-season timing of flights at the northernmost and southernmost extent of the Philippines (question #1). The input data for these tests were the proportion of total flights observed on each observation day (proportion of the total number of birds counted for the season on Day 1, Day 2, etc.). For analytical purposes we designated Day 1 as 25 August for both years. We used the Fligner-Killeen (median) test to evaluate variability of the number of birds observed per day between the sites (Fligner and Killeen 1976). To evaluate within-day patterns between the two count sites, we used another Wilcoxon signed-rank test to compare the proportion of flights per hour, from 0600 H to 15000 H. We used Nemenyi test for post-hoc analyses (Nemenyi 1969).

We described the most commonly observed migration characteristics (directionality, flight altitude) of raptors at each watch site (question # 2). We evaluated, with a binomial generalized linear model, the association of weather parameters (U wind, V wind and percent cloud cover) with the likelihood of observing either a large (≥ 100 migrants/hr) or a small flock (<100 migrants/hr; i.e., the weather conditions under which birds initiate or complete oceanic crossings; question #3). Finally, we used paired Wilcoxon signed-rank tests and Kruskal-Wallis tests to compare timing of passage of the two principal species at each site, by day of year and by hour of day, and binomial generalized linear models (as before) to compare meteorological covariates of their oceanic crossings (question #4). We again used a Nemenyi test for post-hoc analyses. We conducted statistical analyses with R statistical software, using the ‘stats’ package (wilcox.test, kruskal.test, posthoc.kruskal.nemenyi.test, fligner.test and glm (R Development Core Team 2013).

RESULTS

Timing of Migration. We observed 7587 migratory raptors of seven species during 50 d of counting at Basco (Fig. 2a, Table 1). Chinese Sparrowhawk was the most common species recorded, representing 88.8% of the total count. Grey-faced Buzzard was the second most common species at 7.5%, and the remaining migrants were Osprey (*Pandion haliaetus*), Japanese Sparrowhawk (*A. gularis*), Eurasian Kestrel (*Falco* *tinnunculus*), Peregrine Falcon (*F. peregrinus calidus*) and Common Buzzard (*Buteo buteo*; Table 1). Unidentified raptors made up 2.9% of the total. We observed the largest flight of 3653 individuals, which consisted only of *Accipiter* spp., on 9 September 2014 (Fig. 2a). The count from this single day made up 48.1% of the season total. We counted at least 100 raptors on 18% of the count days, but we observed no birds on 24% of the days.

We observed 27,399 migratory raptors of seven species during 47 d of count at Cape San Agustin (Fig. 2b, Table 1). As at Basco, the Chinese Sparrowhawk was the most common species recorded, representing 91.7% of the total count. The Grey-faced Buzzard was the second most common at 7.9%; the remaining migrants were Osprey, Pied Harrier (*Circus melanoleucos*), Japanese Sparrowhawk, Eurasian Kestrel, and Peregrine Falcon (Table 1). Unidentified raptors made up 0.2% of the total. We observed a maximum flight of 2588 individuals, consisting only of *Accipiter* spp., on 28 September 2012 (Fig. 2b), a count that made up 9.4% of the season total. We counted at least 100 birds were counted on 70.2% of the days, with counts of more than 1000 raptors on 5 d. There were no days on which we observed no birds.

Within-season distribution of flights. There was a statistical difference in the within-season distribution of migration, with the majority of individuals passing Basco earlier in the year than that at Cape San Agustin (V = 1165.5, $P < 0.001$; Fig. 2). Although the average daily proportion of flights was the same in Basco (2% of total flights a day) and at Cape San Agustin (2%), the variability in number of birds observed per day was much greater at Basco (SD = 7.42%) than at Cape San Agustin (SD = 2.16%; $\chi 2 = 12.76$, $P < 0.0001$).

Within-day distribution of flights. Migration at Basco began as early as 0530 H, just after local sunrise (Fig. 3). Although we saw sizeable flights between 0700 H to 0800 H (n = 1095 individuals), daily passage rates peaked much later in the day, between 1600 H and 1700 H (n = 1676) and 1700 H and 1800 H (n = 1895), about 30 – 90 min before local sundown. We commonly observed Grey-faced Buzzards searching for and landing at roosting sites during late afternoon.

On most days at Cape San Agustin, migration began at 0700 H –0800 H (Fig. 3), or about 90 min after local sunrise. Flights then peaked between 0800 H to 0900 H (n = 4334) and 0900 H to 1000 H (n = 4531). Few birds were tallied after 1500 H, and departures from the Cape generally ended before 1430 H, or 180 min before local sundown. Differences in within-day timing of flights between Basco (later in the day) and Cape San Agustin (earlier in the day) were statistically significant (V = 45, P = 0.042).

Direction of Migration. Most raptors, 94.5%, passed through Basco in a southerly direction. The majority of birds at Basco (72.3%) approached the coastline at a low altitude.

At Cape San Agustin, 99.6% of birds passed in a southerly direction. Most of the birds migrating past Cape San Agustin (94.6%) departed the coastline at a high altitude

Migration and Weather. At Basco, the winds were from the northeast 41.6% of the time, with hourly wind speeds averaging 4.6 m/sec and reaching a maximum of up to 15.3 m/sec. It was typical to experience such winds in September and October, especially as trade winds and cool northeasterly winds, replaced the southwesterly monsoonal winds. However, passage rate was highest on northwest winds, during which 57.9% of the flights occurred (Fig. 4a). About 9.8% of the flights were into headwinds (southerly winds), and the only species that we observed flying into headwinds were *Accipiters*. Likewise, 10.9% of flights were in northeast winds, 10.8% in westerly winds, 8.5% in easterly winds, 0.8% in north winds, 1% with no wind and 0.2% in variable winds.

At Cape San Agustin, winds were predominantly from the northwest (44.7% of the time) with average hourly wind speeds of 2.5 m/sec and reaching a maximum of 7.8 m/sec. As at Basco, the passage rate at the Cape was highest with northwest winds, when 56.3% of the flights occurred (Fig. 4a). About 11.2% of the flights were into headwinds (southerly winds), nearly all by *Accipiters*; 13.4% of flights occurred with no wind, 11.2% in north winds, 7.2% in variable winds, and 0.2% each in northeast winds, west winds and east winds.

At both sites, passage rate was highest when winds were relatively low. At Basco, winds were usually breezes of 3.4 – 5.5 m/sec (26.6% of the time), but 65.3% of the flights occurred with lighter breezes of 1.6–3.3 m/sec (Fig. 4b). Thus, migration occurred at below-average wind speeds at Basco. At the Cape, hourly wind speeds were mostly very light at 0.3–1.5 m/sec (46.0% of the time) and 42.8% of flights occurred with these winds. Thus, response to wind speed differed between the two sites (W = 2, *P* = 0.008).

The odds of observing a large migratory flock (≥ 100 migrants in an hour) of birds into and out of the Philippines decreased with increasing north winds and, to a small degree, with increasing cloud cover. When all other predictors were held constant, the odds of observing large flocks migrating into Basco changed by a factor of 0.65 (i.e., the odds decreased) for every 1 m/sec increase in V winds (a 1 m/sec increase in V wind is a headwind; Fig. 5). Likewise, the odds of observing large flocks changed by a factor of 0.96 for every 1% increase in cloud cover. As at Basco, when all other predictors were held constant, the odds of observing large flocks departing Cape San Agustin changed by a factor of 0.57 for every 1 m/sec increase of V winds; they changed by a factor of 0.99 for every 1% increase in cloud cover (Fig. 5).

Among-species Differences in Behavior. *Seasonality of the flights.* At Basco, we observed *Accipiters* on 36% of the count days, and Grey-faced Buzzards on 32% of the count days. *Accipiters* and Grey-faced Buzzards had statistically different within-season timing of flights (V = 136, $P = 0.017$) but similar within-day timing of flights (V = 23, $P = 0.233$). Further, *Accipiter* passage (Kruskal-Wallis, $\chi 2 = 49.02$, df = 12, $P < 0.001$) and Grey-faced Buzzard passage (Kruskal-Wallis, $\chi 2 = 44.71$, df = 12, $P < 0.001$) were not evenly distributed throughout all hours of the day. Post-hoc tests showed that *Accipiters* and Grey-faced Buzzards were more likely to pass by the count site in the early morning or afternoon than during mid-day.

At Cape San Agustin, we observed *Accipiters* on 91.5% of the count days, and Grey-faced Buzzards on 42.5% of the count days. *Accipiters* and Grey-faced Buzzards had statistically different within-season timings (V = 694, $P = 0.047$) and within-day timings (V = 0, $P = 0.002$). Additionally, *Accipiter* passage (Kruskal-Wallis, $\chi 2 = 75.75$, df = 9, $P < 0.001$) and Grey-faced Buzzard passage (Kruskal-Wallis, $\chi 2 = 44.71$, df = 12, $P < 0.001$) were not evenly distributed throughout all hours of the day. Post-hoc tests showed that *Accipiters* were more likely to pass in early morning or midday than in the afternoon. Grey-faced Buzzards were more likely to pass during midday or afternoon than in early morning.

Weather. There were among-species differences in correlations of wind speed with migration at both sites. At Basco, 70.6% of *Accipiters* observed passed during light breezes of 1.6–3.3 m/sec, but 66.4% of Grey-faced Buzzard flights occurred during much stronger winds of 3.4–10.7 m/sec. In contrast, at the Cape, 69.2% of *Accipiters* passed during light wind of 0.3–3.3 m/sec, but 82.1% of Grey-faced Buzzards migrated during calmer conditions with winds of <0.3–1.5 m/sec.

At Basco, the odds of observing *Accipiters* increased with tailwinds and eastward winds (Fig. 6a). In contrast, the odds of observing Grey-faced Buzzards increased with headwinds and westward winds (Fig. 6a).

At Cape San Agustin, the odds of observing *Accipiters* increased with tailwinds and eastward winds, and decreased with cloud cover (Fig. 6b). In contrast, the odds of observing Grey-faced Buzzard passage increased with headwinds and cloud cover (Fig. 6b).

DISCUSSION

Our analysis characterizes overwater flight behavior as birds approached and departed coastal areas along an oceanic migration route. Although our data did not allow us to separate year and site effects, the environmental correlates of migration we identify are a useful starting point for understanding the context for open-water crossing by these birds and as a framework for generating hypotheses testable with more detailed count data.

Timing of Flights. Overwater flights started in mornings or midday and ended either early in the morning or late in the day. Although our two seasonal counts were not conducted during exactly the same periods, the pattern we observed was consistent with previous data suggesting that the within-day distribution of raptor flights overwater responds to hourly thermal availability and atmospheric conditions (Spaar 1997, 1999, Meyer et al. 2000, Bildstein et al. 2009, Panuccio et al. 2013). We observed some evidence of successful nighttime migration with a few birds arriving at Basco before or just after local sunrise. Likewise, Germi et al. (2009) and Sun et al. (2010) found little evidence of night flights and believed nocturnal migration to be uncommon along this oceanic route.

Migrants are thought to choose carefully when to initiate overwater crossings and ideally to wait for favorable conditions (Meyer et al. 2000, Liechti 2006, Bildstein et al. 2009, Sjöberg et al. 2015). With favorable conditions (i.e., strong tailwinds or weak headwinds) birds traveling in the Philippines likely start migration early in the day and take about 3 hr to cross the ocean. We suspect that afternoon arrivals into Basco were probably of migrants that were delayed in leaving the southern tip of Taiwan or took longer than anticipated to cross the ocean. Kerlinger and Gauthreaux. (1984) and Panuccio et al. (2013) suggest that afternoon completion of water crossings may be intentional behavior by migrants that intend to roost on the islands. On Basco, this appears to be the case as we observed large roosting assemblages on the island (C Concepcion and K. Bildstein unpubl. data).

Meteorological and Behavioral Correlates of Ocean Crossing Flights. The migration we observed by birds approaching and departing the Philippines was generally southward (i.e., expected flight direction). Reversed or unexpected flight directions were uncommon in the Philippines, although it is a common occurrence at many other sites (Alerstam 1978, Åkesson et al. 1996, Nilsson and Sjöberg 2015). Migrants may fly in other directions when they are hesitant to cross a barrier (such as the open ocean from

Cape San Agustin), when fuel reserves are low, or when weather conditions encountered are unfavorable.

The raptor migration we observed through and out of the Philippines coincided with certain meteorological patterns. In particular, the odds of observing migrants showed a positive relationship to tailwinds (lower headwinds) and were slightly negatively correlated to cloud cover. Cloud cover at the coast is likely important because it may reduce thermal availability (Spaar 1999). Cloud cover may also have caused us to miss birds, especially those flying above the clouds (Richardson 1978, Kahlert et al. 2012). Tailwinds are likely to speed up overwater crossings (Alerstam 1990, Meyer et al. 2000, 2003). In the Philippines (see Fig. 1), migrants undertaking lengthy overwater crossings are believed to use northeasterly Trade Wind Zone tail winds to help complete their passage (Bildstein 2006). Northeasterly winds along this flyway peak between July and October and extend from 5° to 30° N. However, these winds are particularly strong between 15° and 20° N, a latitudinal band that includes the Basco watchsite but not the Cape San Agustin watch site (Wyrtki and Meyers 1975). Thus the migrants we observed at Basco likely benefitted more from trade tail winds than the migrants we observed at Cape San Agustin. The migrants we counted at Cape San Agustin instead may rely on seasonal winds and sea thermals to subsidize their overwater migratory flights (Bildstein 2006). Sea thermals, in particular, occur in tropical and subtropical waters between 5° to 30° north and south of the equator (Augstein 1980) and would be available for migrants observed at both Basco and at Cape San Agustin.

Although tailwinds favored migration at our sites and also in Sangihe, Sulawesi, Indonesia (Germi et al. 2009), Grey-faced Buzzards we observed often flew into headwinds. The decision to fly into headwinds may result in higher-than-normal energetic expenditures (Meyer et al. 2000). Thus, it may be that these Grey-faced Buzzards may have been forced to migrate to avoid still worse weather conditions (*cf.* Liechti et al. 2013) or they may be travelling short enough distances that the additional energy expended in headwinds may be of relatively little consequence (Germi et al. 2009).

Species Differences in Flight Behavior. We recorded interspecific differences in timing and weather correlates of overwater crossings. Explanations for among-species differences such as these include variation in flight mechanics (Mendelsohn et al. 1989, Hedenström 1993) and individually based strategies in response to the environment (Spaar 1997, 1999, Meyer et al. 2000). In general, smaller raptors with longer, narrower wings are more adapted to flapping flight than are larger raptors. Such birds are also more likely to cross large water bodies (Kerlinger 1985, Meyer et al. 2000). This difference might explain why the relatively small, and long, narrow-winged *Accipiters* and Grey-faced Buzzards we observed make up the bulk of migrants using the East-Asian Oceanic Flyway. Individuals of these species would be able to easily switch between soaring and flapping flights in response to local variation in weather.

Overwater Crossing as an Influence on Raptor Migration. When birds make mistakes overwater, they often are not easily corrected and many times are fatal (Bildstein 2006, Bildstein et al. 2009, Oppel et al. 2015). Young birds are relatively more likely to make such mistakes and so survival of their maiden voyages across the ocean may depend on following the lead of experienced adults (Agostini et al. 2010, Panuccio et al. 2012, Oppel et al. 2015). For example, when the number of adults in the population declined, only 1 in 10 young Egyptian Vultures (*Neophron percnopterus*) survived their first migration across the Mediterranean Sea (Oppel et al. 2015). We frequently observed large flocks of migrants and it may be that these were composed of knowledgeable adults being followed by inexperienced juveniles. Further insight into this question may come from comparison of flock size and adult: subadult ratios among populations of raptors that do and do not make oceanic crossings.

Our study is one of a few that has focused on understanding migratory strategies across the world's only "true" large-scale oceanic flyway (Bildstein 2006). Our findings are preliminary and suggest the hypothesis that similar general meteorological conditions favor initiation and completion of overwater crossings during autumn migration. These observations are particularly important because so few overwater crossings have been studied, especially outside the European Baltic and Mediterranean regions and more data would be valuable to more fully test these initial hypotheses.

In addition, it would be useful to replicate our study during spring migration along this corridor. In spring, northeast trade winds remain strong north of the equator, starting from about 5° N. However, south from 5° N, southeast trade winds are strong (Wyrtki and Meyers 1975). This means migrants would face strong headwinds as they cross from Indonesia to the south of the Philippines and would likely encounter such headwinds until they pass the southern tip of the Ryukyu Islands of Japan, roughly around 30° N. Given these realities, migrants may therefore abandon the oceanic flyway and instead follow a loop migration pattern via the East-Asian Continental Flyway, where the southeast trade winds would actually assist their return migration. Count data from southern Taiwan seem to support this prediction (Lin and Severinghaus 1998). Future studies using telemetry will be important for understanding these patterns.

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Table 1. Migratory raptors counted at Basco (25 August – 19 October 2014) and Cape San Agustin (12 September – 30 October 2012), Philippines.

COMMON NAME	SCIENTIFIC NAME	BASCO	CAPE SAN AGUSTIN
Osprey	*Pandion haliaetus*	7	2
Pied Harrier	*Circus melanoleucos*		1
Japanese Sparrowhawk	*Accipiter gularis*	14	17
Chinese Sparrowhawk	*A. soloensis*	6737	25,126
Grey-faced Buzzard	*Butastur indicus*	571	2176
Eurasian Kestrel	*Falco tinnunculus*	18	6
Peregrine Falcon	*F. peregrinus calidus*	9	16
Common Buzzard	*Buteo buteo*	5	
Unidentified accipiter	*Accipiter* spp.	178	24
Unidentified falcon	*Falco* spp.	1	2
Unidentified raptors		47	29
TOTAL		**7587**	**27,399**

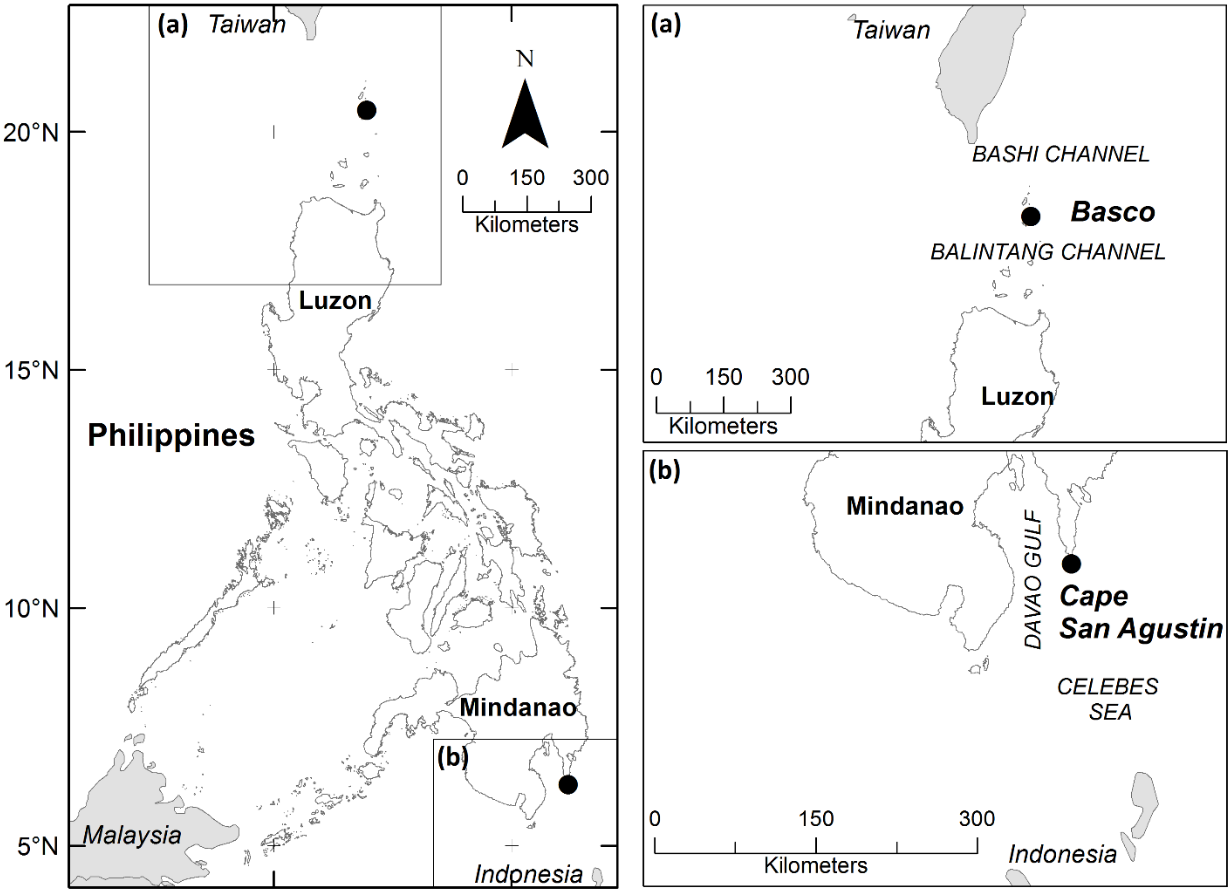

Figure 1. Geographic locations of watchsites in the Philippines where migration counts were conducted in 2012 (Cape San Agustin) and 2014 (Basco). Map on the left shows the entire Philippines with the location of watchsites (●). The top right inset (a) shows the location of the watchsite at Basco and part of Taiwan, which is 180 km north, and mainland Luzon of the Philippines, 280 km south. The bottom right map (b) shows the location of the watchsite at Cape San Agustin found in the island of Mindanao, as well as the northernmost islands of Indonesia (Sulawesi), 170 km south.

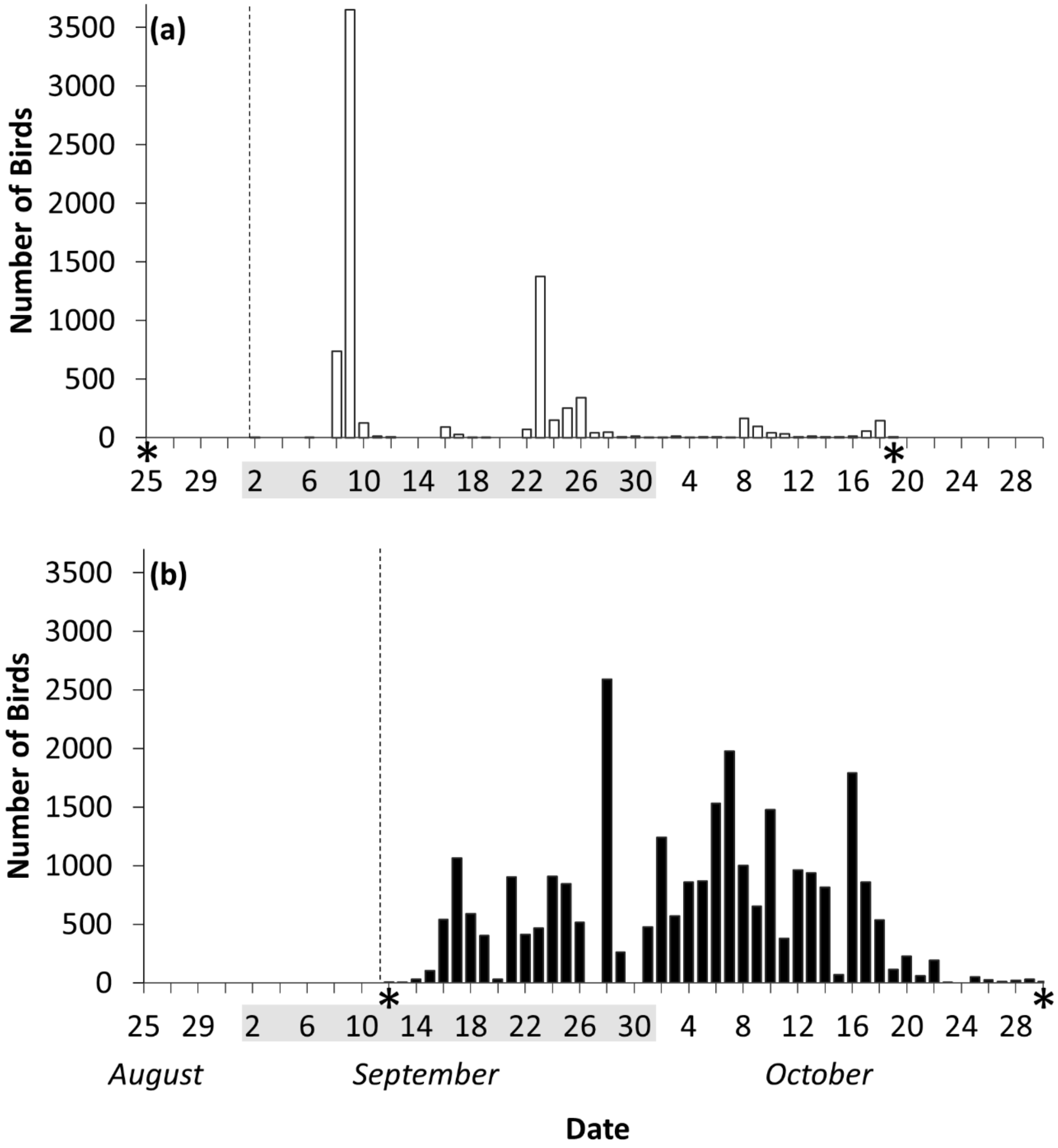

Figure 2. Within-season distribution of autumn migration flights observed at (a) Basco (25 August – 19 October 2014) and (b) Cape San Agustin (12 September – 30 October 2012), Philippines. Vertical dashed line shows the first day that migration was observed. Asterisks show the first and last days of count. These data did not allow us to assess interannual variation in migration behavior. Because sampling periods were not identical, the start and end of some seasonal distributions may not be represented in these data.

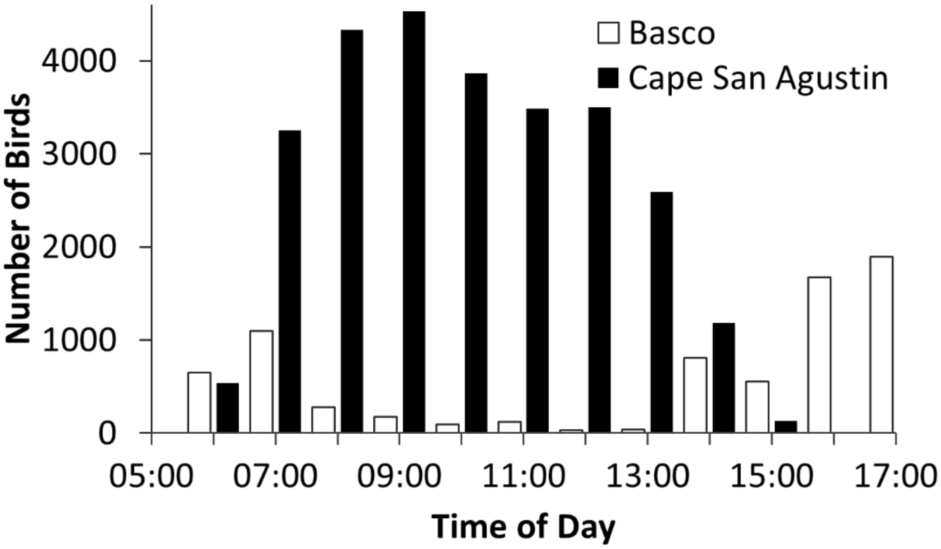

Figure 3. Time of day of autumn migration flights observed at Basco (25 August – 19 October 2014) and Cape San Agustin (12 September – 30 October 2012), Philippines. Migration flights were observed from 0530 H to 1730 H (Basco) and 0600 H to 1530 H (Cape San Agustin).

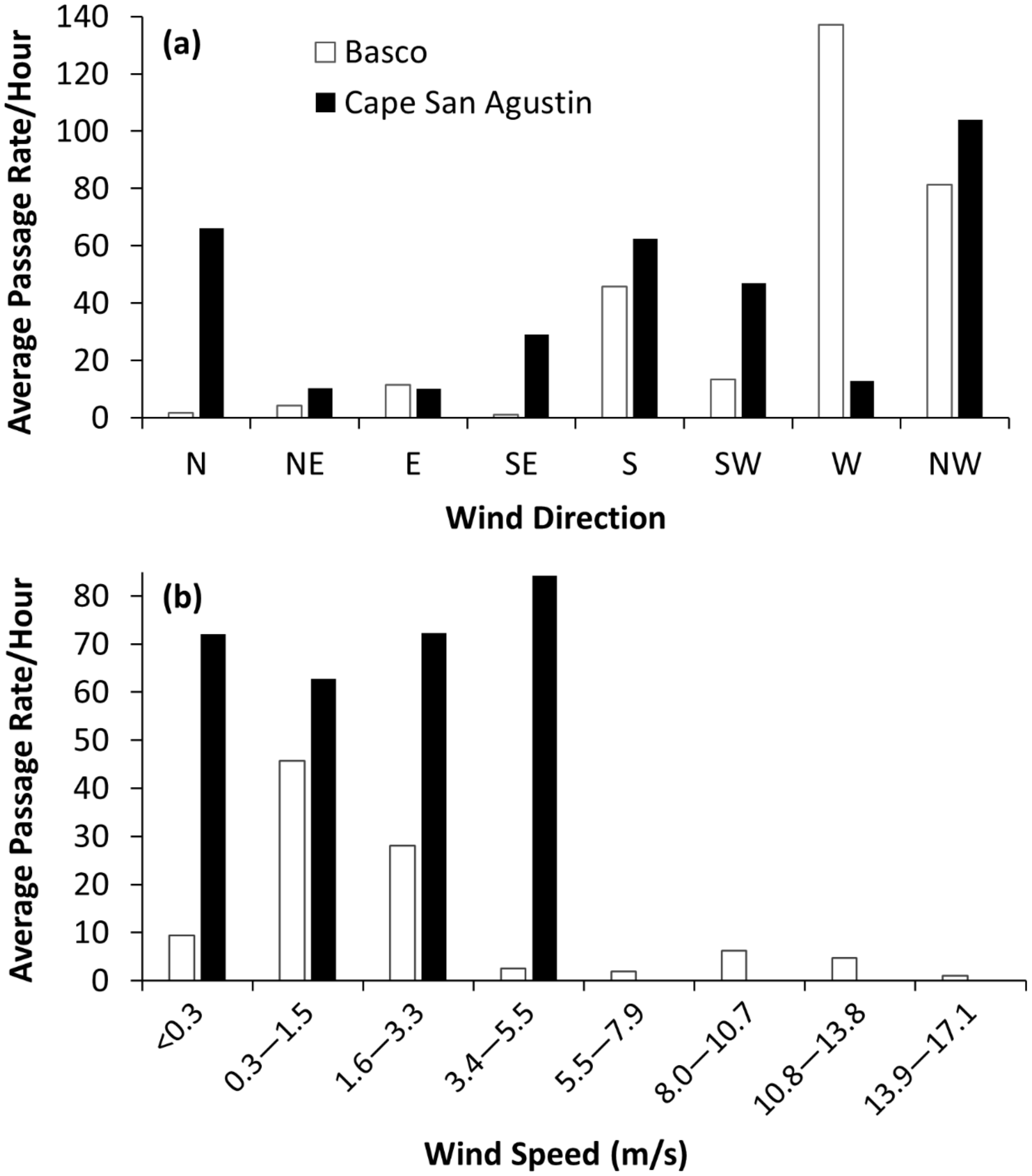

Figure 4. Average passage rates of all raptors counted per hour during different (a) wind directions and (b) wind speeds (m/sec) during autumn migration at Basco (25 August – 19 October 2014) and Cape San Agustin (12 September – 30 October 2012), Philippines. Standardized categories for wind speeds were based on the Beaufort scale (Hasse 2015).

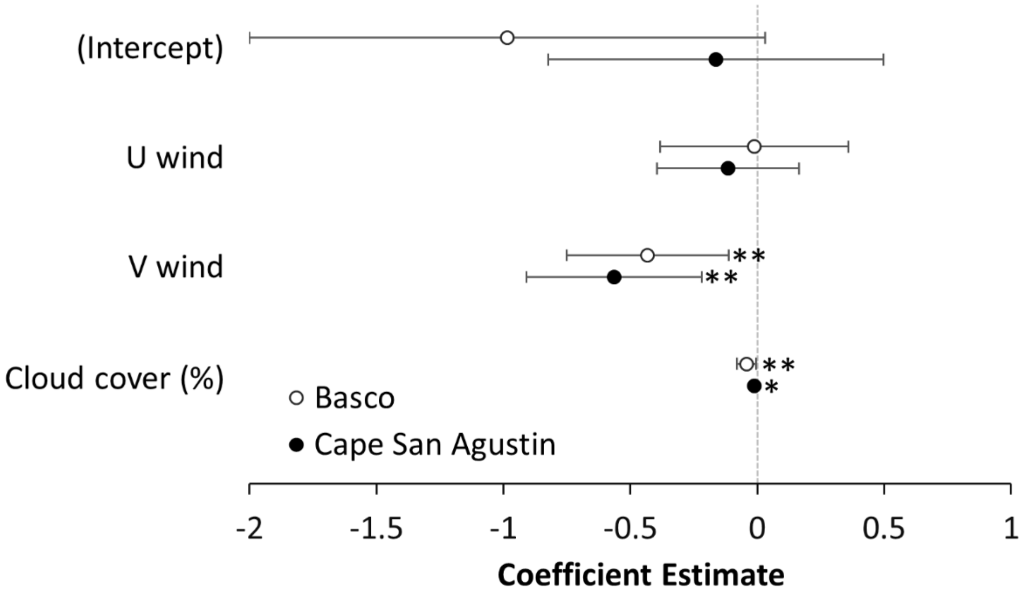

Figure 5. Coefficient estimates for generalized linear mixed models for weather conditions associated with hourly autumn passage rates for Basco (25 August – 19 October 2014) and Cape San Agustin (12 September – 30 October 2014), Philippines. U and V wind components were measured using handheld, digital anemometer. Cloud cover was the estimated percent of sky with background cloud cover. Bars represent 95% confidence intervals. Statistical significance indicated by number of asterisks: * indicates *P* <0.05, ** indicates *P* <0.01, *** indicates *P* <0.001)

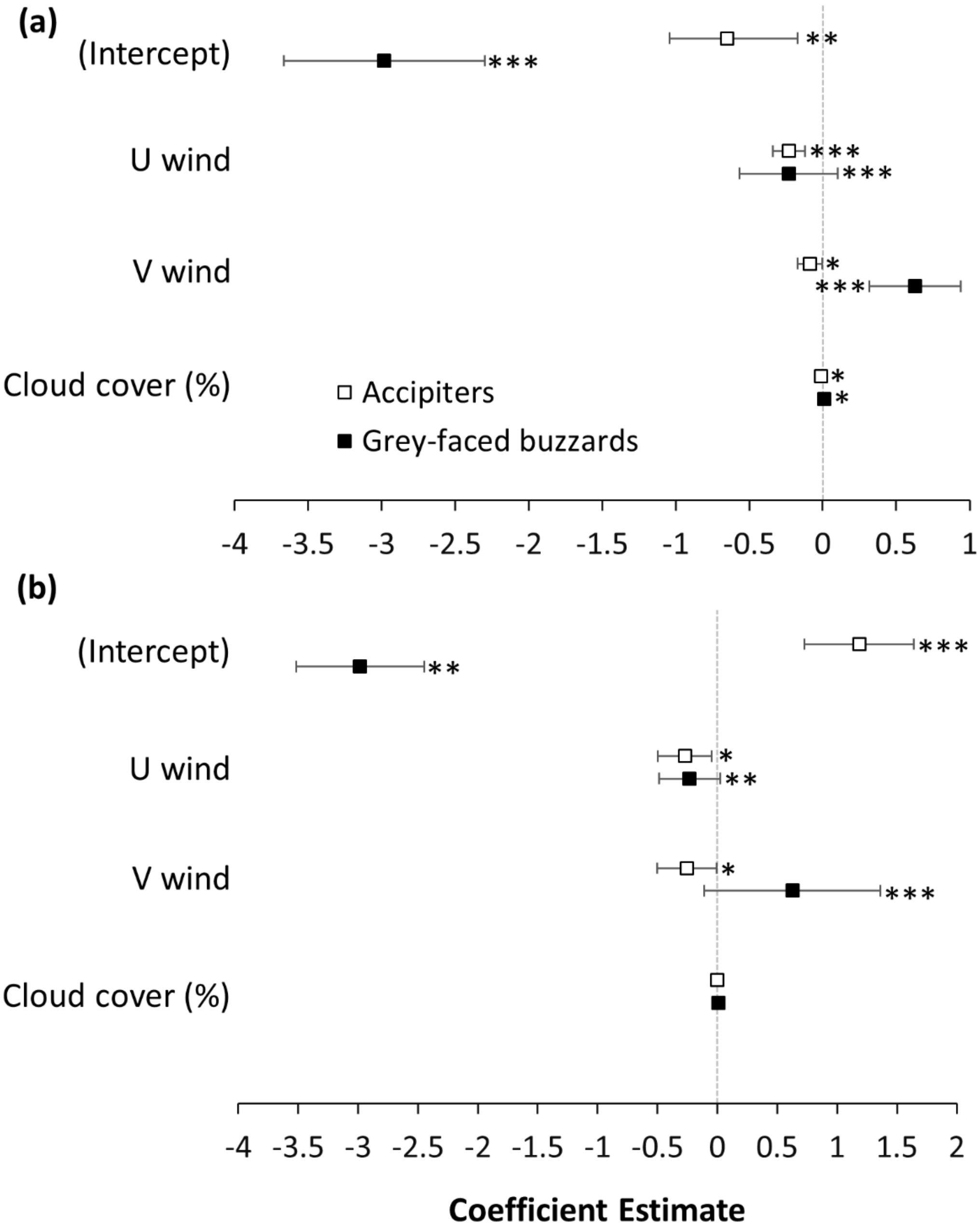

Figure 6. Coefficient estimates for generalized linear model for weather conditions associated with Accipiter and Grey-faced Buzzard hourly autumn passage rates for (a) Basco (25 August – 19 October 2014) and (b) Cape San Agustin (12 September – 30 October 2012), Philippines. U and v wind components were measured using handheld, digital anemometer. Cloud cover was the estimated percent of sky with background cloud cover. Bars represent 95% confidence intervals. Statistical significance indicated by number of asterisks: * indicates *P* <0.05, ** indicates *P* <0.01, *** indicates *P* <0.001).

CHAPTER 4

Abundance of island avian predators in a heavily impacted tropical forest suggests that endemics face greatest risk from landscape changes

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ABSTRACT

Anthropogenic land cover change is among the largest threats to biodiversity, and island endemics and habitat specialists are especially vulnerable to these changes. We used road surveys and occupancy modeling to determine the distribution of birds of prey in the southern Philippine island of Mindanao and to assess the land cover characteristics that influence this distribution. During winter field surveys between 2014 and 2016, we observed 13 of the 27 birds of prey species present on Mindanao and we counted 1,656 individuals. The Brahminy Kite (*Haliastur indus*) and the Philippine Serpent Eagle (*Spilornis holospilus*) were the most commonly observed species. Our models suggest that on average, detection probability was 86% for all raptors combined, 50% for Brahminy Kites, and 35% for Philippine Serpent Eagles. Our models also predict that the probability of occupancy by Brahminy Kites (a purported habitat generalist with a large distribution) was positively correlated with forest disturbance while probability of occupancy by Philippine Serpent Eagles (an endemic and purported forest specialist) was highest in near-pristine forests. Further, we observed fewer island endemics and more non-endemic residents than predicted by our models. These suggest that the anthropogenic changes in central and eastern Mindanao are more consequential to endemics than expected and that endemics are more vulnerable to these changes than are more widespread species.

INTRODUCTION

Anthropogenic landscape change is among the greatest threats to global biodiversity. The expansion and intensification of agriculture, in particular, have been predominant drivers of this process (Matson et al. 1997, Clay 2004). Land cover change leads to the loss of natural environments, alters structure and function of ecosystems (Vitousek et al. 1997, Foley et al. 2005), and removes, reduces, or isolates suitable habitats (Fahrig 2003). Altogether, these changes can decrease the capacity of the environment to support biodiversity (Gaston et al. 2003). As a result, although species and community response to land cover change is highly context-specific (Hansen et al. 2001), human-modified environments almost always support smaller populations of lower species diversity than do unmodified environments (Rapport et al. 1985, Gardner et al. 2008).

For birds, habitat fragmentation can influence spatial and temporal changes in populations by affecting territory size and dispersal (Rolstad 1991). As predators, raptors have smaller populations than most other avian species, they occur at lower densities, they are dependent on movements of their prey, and they are often a focus of persecution by humans (Newton 1979, 1998, Thiollay and Meyburg 1988, Hall et al. 2015). As a consequence, raptors, particularly forest raptors, often are especially vulnerable to landscape changes (Jullien and Thiollay 1996, Thiollay 2007).

These patterns are especially true for raptor communities in islands, where endemism is high (Gentry 1992, White and Kiff 2000), and species occur in naturally constrained ranges (i.e. limited to the size of the island) and have restricted potential to disperse (Thiollay and Meyburg 1988, Virani and Watson 1998, Blackburn and Gaston 2002). As a result of anthropogenic landscape changes, tropical island endemics are among the most globally threatened raptors in the world (Concepcion et al. 2017).

The Philippines has one of the planet's richest and most threatened areas of biodiversity (Myers et al. 2000, Hannah et al. 2013). The archipelago has such high rates of deforestation (Lasco and Pulhin 2000, Bankoff 2007) that only 3% of its original primary forest remains (Myers et al. 2000). Deforestation affects many of the country's 29 species of diurnal birds of prey, 15 of which tend to occupy habitats with more than 50% forest cover (Gamauf et al. 1998, Kennedy et al. 2000). Among Asian countries, the Philippines also has among the highest number of endemics and globally threatened species make up a disproportionately large proportion of the species present (Concepcion et al. 2017).

To understand the effects of changes in land cover on tropical raptor communities and species, we surveyed raptors and land cover types in central and eastern areas of the Philippine island of Mindanao. We used these data to identify the distribution of birds of prey present and to assess how land cover characteristics has influenced this distribution. Our specific objectives were to (1) evaluate patterns in raw count data to understand how road surveys compare to other survey techniques that have been used, (2) describe the abundance of raptor and habitat relationships of raptor communities within central and eastern Mindanao, and (3) characterize among-species (forest specialist vs habitat generalist) differences in landcover correlates of occupancy.

METHODS

Study area

The Philippines is a tropical, southeast Asian archipelago made up of over 7,000 islands with an area of 300,000 km^2. Its land cover is a mosaic of rainforests, croplands and plantations (Catibog-Sinha and Heaney 2006). The few remaining forests that have not been cleared for agriculture are found mostly on the islands of Palawan, Mindanao, and the northern and southern parts of Luzon. These forests are one of three types, low-elevation dipterocarp, high elevation montane, or mangrove. Low elevation dipterocarp forests are usually found from sea level up to 700 meters above sea level (ASL; Heaney 1998, Catibog-Sinha and Heaney 2006), although in Mindanao, dipterocarp forests sometimes extend up to 1,500 meters ASL. Dipterocarp forests are dominated by large trees in the family

Dipterocarpaceae that have massive supporting buttresses, and can grow up to three meters in diameter and 60 meters tall. Lianas (woody vines), other vines and strangler fig trees (*Ficus* spp.) are common. High elevation montane forests on Mindanao are usually found at 700 - 2,300 meters ASL. Montane forests are dominated by oak (*Quercus* spp.) and laurels (Lauraceae family) that grow up to 25 meters tall. These trees are covered in moss and epiphytes, such as pitcher plants (*Nepenthes* spp.), orchids (Orchidaceae family), and palm (*Freycinetia* spp.). Mangrove forests are exclusively coastal in distribution.

We surveyed for raptors in representative portions of land controlled by five towns of the island of Mindanao (Figure 1). These areas were selected because they were accessible (parts of Mindanao are contested and not safe for travel) and represented a diversity of forest types, disturbance regimes, and elevations (Ong et al. 2002, Conservation International - Philippines et al. 2006). They are:

- *Lantapan*, in the Province of Bukidnon, has near-pristine, high elevation montane forests located within the Mount Kitanglad Range (312 km^2). The forests there are surrounded by a matrix of agricultural and open lands. Mount Kitangland Range has national protected status.
- *Arakan*, in the Province of North Cotabato, has severely disturbed, high elevation montane forest, confined to the slopes of Mt. Sinaka (17 km^2). Similar to Lantapan, the forest in Arakan is surrounded by a matrix of agricultural and open lands.
- *Davao City*, in the Province of Davao del Sur, has moderately disturbed, high elevation montane forest. The 41 km^2 of forests here are surrounded by open and agricultural lands and are located within the Marilog Forest Reserve.
- *San Isidro* and *Governor Generoso*, both in the Province of Davao Oriental, are neighboring towns and share 319 km^2 of contiguous, low elevation Dipterocarp forests found within the protected Mt. Hamiguitan Range Wildlife Sanctuary. The forest we surveyed near San Isidro is near-pristine,

while the forest we surveyed near Governor Generoso is moderately disturbed.

Survey techniques

In each town, we surveyed for raptors at 11 point counts distributed at 1-km intervals along a fixed, 10-km transect. Each transect was established along existing roads and we used GoogleEarth and local information to select those roads that crossed or ran adjacent to forest for the longest distance. We began the transect where the road dead-ended.

Surveys were completed in November to December of 2014, 2015, and 2016. Each year, the five routes were sampled five times over a three-day period. Surveys occurred up to twice per day, starting as early as 0900H and finishing at or before 1600H, approximately the period during the day when rain forest birds are most likely to soar and perform territorial or display flights (Thiollay 1989). Due to logistical constraints, we did not have equal numbers of morning and afternoon surveys. We drove each of the five 10-km transects five times in each of three years, covering a total of 750 km.

At each point count location, four observers exited the car, fanned out along the point, and surveyed for raptors for 10 minutes. We spotted raptors by using binoculars, field scopes and the unaided eye to methodically scan the sky and trees. For each bird sighted, we recorded the route, observer location, species, time of sighting, straight line distance from observers, activity (flighted, perching) and the land cover type where the bird was detected (forest, forest edge, open, agricultural). We assumed that flight activity was for territorial display. Whenever possible, we estimated the age of the individual as either immature or adult. Observers shared information and any bird spotted was only recorded once.

Finally, at each point count, we noted the forest type (dipterocarp or montane), and level of disturbance (low, moderate, severe). Disturbance was characterized based on logging history, area of forest remaining, and human activity surrounding the remaining forest. In general, low disturbance sites were unlogged and were rarely used by humans. Moderately disturbed sites had been logged on the periphery and had some agricultural activity around the remaining forest. Severely disturbed sites had been heavily logged and remaining forest fragments were surrounded by extensive agriculture. We did not have access to a severely disturbed, dipterocarp forest.

Data analysis

We used our observations at point counts to build year-specific encounter histories. We then used *N*-mixture models for spatially repeated counts (Royle 2004) within Program MARK (Version 6.2, Dec. 2016; White and Burnham 1999) to estimate detection and occupancy probabilities of the raptors we counted. These models estimate, through a logit likelihood function, the binomial sampling probability that a particular individual is detected (*r*), and the Poisson intensity parameter of occupancy (λ) at each point (Royle and Nichols 2003, Royle 2004). Intensity parameter estimates the number of individuals at each point count. Global detection and transect-specific occupancy probabilities were calculated from these parameters.

In our models, we set the intensity (λ) and individual detection probability (*r*) parameters to be either constant or we allowed them to vary among the three survey years. Our model set included four models, with all possible combinations of individual detection and intensity parameters, as follows:

- *r* and λ constant over time
- *r* constant over time and λ time-varying
- *r* time-varying and λ constant over time; and
- *r* and λ time-varying.

In all our models, we allowed λ to be influenced by forest type and level of disturbance. To reduce deviances, we applied a global optimization with simulated annealing (Goffe et al. 1992). We model averaged across all models in each set

(Doherty et al. 2012) to estimate model parameters (Buckland et al. 1997, Burnham and Anderson 2002).

To evaluate patterns in raw count data (for objective #1), we used Kruskal-Wallis test and Wilcoxon signed-rank tests, within R statistical software (R Development Core Team 2013) to compare between years, times of day (0900—1200H vs 1300—1400H), and forest types, the raw count data on numbers of raptors counted on surveys at each survey point. To describe where we detected raptors and how those detections were distributed in our survey areas (objective #2), we adjusted those raw count data with region-specific model averaged detection and occupancy probabilities. Because we observed relatively few birds of most species, we could not model detection and occupancy probabilities for each species individually. Instead, to describe the general patterns for this guild, we estimated detection and occupancy probabilities (as described above) for all raptors combined (Duerr et al. 2015). We then use these detection and occupancy estimates to evaluate among-forest differences in patterns of raptor occupancy.

To identify differences among occupancy patterns for the two most-commonly observed species (objective #3), again we first used Wilcoxon signed-rank tests to compare between survey years, time of day (AM vs PM), and forest types, the raw count data on numbers of individuals. We then again adjusted those raw count data with model averaged detection and occupancy probabilities. Finally, we used these detection and occupancy estimates to evaluate among-forest differences in patterns of occupancy of those two species.

RESULTS

Raptor communities within central and eastern Mindanao

Between 2014 and 2016, we observed 13 species of birds of prey and 1,656 individual raptors (Table 1). Four species were Philippine endemics, three were migrants that do not breed in the Philippines, five species were habitat generalists, and five were forest specialists (Table 1). The Brahminy Kite (*Haliastur indus*) and Philippine Serpent Eagle (*Spilornis holospilus*) were the most common species observed. The majority (95%; n = 1,567) of raptors observed were in flight. We observed no inter-annual variation in the number of birds we detected (Kruskal-Wallis, $\chi 2 = 0.57$, df = 2, p = 0.75), but we observed more raptors during morning surveys ($\bar{x} = 3.03$, SD = 1.03) than during afternoon surveys on the same routes ($\bar{x} = 2.42$, SD = 0.94; W = 930, p = 0.01). Further, we observed no variation in the number of raptors we counted among the different forest types (Figure 2, W = 731, p = 0.55).

In general, individual detection probabilities for all raptors were low and intensity of occupancy parameters were high. Global detection probabilities were generally high (0.84 – 0.87) and occupancy probabilities always were approximately 1. For all raptors considered together, there was less support for models that described detection and occupancy probabilities varying among the three survey years (detection: ΣAICc weight = 0.36, occupancy: ΣAICc weight = 0.24) than for models where these remained constant among the years (detection: ΣAICc weight = 0.64, occupancy: ΣAICc weight = 0.76; Table 2, Table 3).

Our model estimated that for every point count within the landcover type the model used as reference (dipterocarp forest with low to moderate disturbance), 12 raptors were present and average detection rates for those raptors were 86%. These models also suggested that within both forest types, disturbance reduced abundance of raptors within forests (Table 4). That said, when disturbance was similar, abundance of raptors was greatest in high elevation montane forests and lower in low elevation dipterocarp forest.

Among-species differences in detection and occupancy

We observed no inter-annual or diel variation in the numbers of Brahminy Kites (year: Kruskal-Wallis, $\chi 2 = 0.67$, df = 2, p = 0.73; time of day: W = 744, p = 0.46) and Philippine Serpent Eagles (year: Kruskal-Wallis, $\chi 2 = 2.41$, df = 2, p = 0.33; time of day: W = 585.5, p = 0.37) that we counted. We observed more Brahminy Kites during surveys around montane forests ($\bar{x} = 2.38$, SD = 0.97) than during surveys around dipterocarp forests ($\bar{x}$ = 1.47, SD = 0.37; W = 224, $p < 0.001$, Figure 2). On the other hand, we observed more serpent eagles during surveys around dipterocarp forests ($\bar{x}$ = 2.09, SD = 0.88) than during surveys around montane forests ($\bar{x}$ = 1.50, SD = 0.58; W = 732.5, p = 0.004, Figure 2).

Our model estimated that at every point count around the reference landcover, there were 6 Brahminy Kites of which 60% were detected. For Brahminy Kites, detection probabilities were relatively high and there was more support for models where this varied among survey years (ΣAICc weight = 0.73) than for models where detection was constant (ΣAICc weight = 0.27; Table 2, Table 3). There was more support for models that described occupancy probability as constant across years (ΣAICc weight = 0.62) than for models where it varied among the years (ΣAICc weight = 0.38;). If disturbance was similar, kites were more likely to occupy dipterocarp forests, than montane forests (Table 4). However, within both forest types, there were 2-3 times more kites in moderately disturbed forests than the other sites.

For Philippine Serpent Eagles, detection probabilities were relatively low and there was more support for models where detection varied among survey years (ΣAICc weight = 0.54) than for models where it was constant among years (ΣAICc weight = 0.46; Table 2, Table 3). There was more support for models where occupancy was constant (ΣAICc weight = 0.57) than models where occupancy varied among the years (ΣAICc weight = 0.43). Based on our model, when disturbance is similar, serpent eagles were more likely to occupy low elevation dipterocarp forests, than montane forests (Table 4). That said, within both forest types, disturbance reduced abundance of serpent eagles within forests. Our model estimated that at every point count around the reference landcover, 8 Philippine serpent eagles were present of which 35% were detected.

DISCUSSION

Understanding the impacts of habitat fragmentation and loss on biodiversity is essential to conserving wildlife populations. To do this, it is crucial to understand how species respond to landscape changes. Our study is among the first to use the combination of road surveys and occupancy modeling to describe communities of birds of prey in either the tropics or the Philippines. More broadly, it also illustrates how island endemics may be relatively more vulnerable to land-use changes than more broadly distributed non-endemic species.

In the course of our surveys, we observed 45% of the total diversity of species of diurnal birds of prey regularly observed in the Philippines. Although detection rates were high, the majority of the birds we observed were in soaring flight and it is likely that we missed species that do not soar. For example, Besras (*Accipiter virgatus*) are known to stay in forests or in the understory and we did not count any of them in our surveys (Gamauf et al. 1998). We also observed more birds during our morning surveys, possibly demonstrating time-of-day patterns in territorial and foraging flight activities (Wakeley 1978, Newton 1979, Ballam 1984).

In the tropics, there are typically more species found in low elevation than high elevation areas (Goodman and Gonzales 1990, Peterson et al. 2000). However, our models suggested the opposite - that few birds occupied low elevation forests. Human population density in the Philippines is greater at low elevations and the patterns we observed likely reflect the greater magnitude of anthropogenic changes at low, as opposed to high, elevation forests (Vester et al. 2007, Nogués-Bravo et al. 2008). In fact, we observed up to 150% more raptors than our model estimated at a high elevation field site (i.e. Davao City). This was unexpected because this site was not only high elevation, but also had moderately disturbed forests. We encountered similar numbers of birds of prey here as we did in a site which had near-pristine, low elevation forest (i.e. San Isidro).

Overall, we observed fewer forest specialists and more habitat generalists than our models predicted. In our study, forest specialists were represented by Philippine

Serpent Eagles which typically occupy dipterocarp forests with over 50% canopy cover (Gamauf et al. 1998, Kennedy et al. 2000, Ferguson-Lees and Christie 2001). Habitat generalists were represented by Brahminy Kites, a species that occupies open cover types. The low numbers of forest specialists and high numbers of habitat generalists may mean one of at least two things. One, forest specialists are forest interior species and road surveys, which use transects that do not always cross the forest, are not an appropriate method to survey for them. Two, our road surveys accurately captured the status of the raptor population, and the remaining forests are highly degraded and therefore, less suitable for forest specialists.

We can test the first of these two hypotheses (that our results are driven by bias induced by the type of survey we conducted) by comparing trends in our data with those from other surveys conducted differently. For example, the most commonly used method for surveying birds of prey in the Philippines is to count birds from a fixed observation point on a ridgetop. Such vantage points provide better views of forested areas than do road surveys. If our survey methods are driving our results, we would expect to observe relatively more forest specialists during surveys from those ridge-top observation posts. However, when concurrent observations from fixed posts and road surveys are conducted, fewer raptors, forest specialists or otherwise, are observed from fixed observation posts (CBConcepcion unpubl. data). Thus, it seems unlikely that survey type is driving the trend we observed.

We can test the second hypothesis (that remaining forests are less suitable for forest specialists) by comparing the numbers of birds of each type that we counted. Based on our detection probabilities and the estimated number of individuals present at each point, we have recorded only 86% of serpent eagles, but 242% of the Brahminy Kites estimated. As these species have opposite landcover needs, these data seem to support our second hypothesis. This finding is especially significant because the Philippine Serpent Eagle is an endemic species, and our results would coincide with Ferrer-Sánchez and Rodríguez-Estrella (2015) who found that "[island] endemics do not cope well with habitat changes." Several other studies have found this to be true for island species (Thiollay and Meyburg 1988, Jullien and Thiollay 1996, Bildstein 1998, Thiollay 1998, Virani and Watson 1998, Sodhi et al. 2004, 2008, 2010). These species may therefore be more vulnerable than are more widespread, generalist species and, if deforestation continues at its current rate, their conservation status, which is currently "Least Concern", may need to be reconsidered.

Our study shows that conducting relatively inexpensive, and statistically robust surveys can be used to assess the impact of anthropogenic land-use change on Philippine wildlife. Although responses to these changes are species-specific (Hansen et al. 2001), our data illustrate that loss of natural environments impacts endemic species. This is directly relevant not just for the Philippine Serpent Eagle, but for the other endemic diurnal raptor species we observed as well. The Philippine Eagle (*Pithecophaga jefferyi*), the Philippine Honey-buzzard (*Pernis stereei*), and the South Philippine Hawk-eagle (*Nisaetus pinskeri*), are all forest specialists. We also found that endemics and habitat specialists, no matter how common, became limited to natural or less disturbed areas. Further investigation will help identify the demographic responses of these species to the continued landscape changes occurring in an already degraded forest areas.

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Table 1. Number of birds of prey observed around central and eastern Mindanao, 2014-2016. Surveys were conducted between November and December each year. Standard deviations are provided. Conservation status are based on IUCN (BirldLife International 2017) and are either Least Concern (LC), Endangered (EN) or Critically Endangered (CR). Migratory status is either resident (R) or Migratory (M). Habitat specialists (S), habitat generalists (G), and “intermediate” species (I) are also identified.

	Status	Distribution	Migratory status	Habitat use patterns	Number of individuals				
					2014	2015	2016	Total	Mean
Black-winged Kite *Elanus caeruleus*	LC	Global	R	G	1	0	1	2	0.002 (0.001)
Brahminy Kite *Haliastur indus*	LC	Asia	R	G	240	258	359	857	1.04 (1.68)
Chinese Sparrowhawk *Accipiter soloensis*	LC	Asia	M	I	2	6	2	10	0.01 (0.12)
Crested Goshawk *Accipiter trivirgatus*	LC	Asia	R	S	0	2	0	2	0.002 (0.05)
Grey-faced Buzzard *Butastur indicus*	LC	Asia	M	G	34	48	26	108	0.13 (0.45)
Oriental Honey-buzzard *Pernis ptilorhynchus*	LC	Asia	M/R	I	12	17	17	46	0.06 (0.34)
Osprey *Pandion haliaetus*	LC	Global	M	G	0	2	2	4	0.005 (0.07)
Peregrine Falcon *Falco peregrinus*	LC	Global	M/R	I	2	4	2	8	0.01 (0.10)
Philippine Eagle *Pithecophaga jefferyi*	CR	Endemic	R	S	4	1	2	7	0.01 (0.09)
Philippine Honey-buzzard *Pernis stereei*	LC	Endemic	R	S	0	4	18	22	0.03 (0.46)
Philippine Serpent Eagle *Spilornis holospilus*	LC	Endemic	R	S	160	143	117	420	0.51 (1.05)
South Philippine Hawk-eagle *Nisaetus pinskeri*	EN	Endemic	R	S	8	10	0	18	0.02 (0.20)
White-bellied Sea Eagle *Haliaeetus leucogaster*	LC	Asia	R	G	4	4	14	22	0.03 (0.21)
Unidentified raptor					42	51	25	118	
Totals					**509**	**550**	**585**	**1644**	

Table 2. Model selection table describing detection probability and occupancy of birds of prey around central and eastern Mindanao. These models estimate intensity (λ) and individual detection probability (r) parameters. We set individual detection probability and occupancy to be either constant ($r_{constant}$ or $\lambda_{constant}$) or to vary among the three survey years (r_{time} or λ_{time}). We allowed the intensity parameter to be influenced by forest type and level of disturbance. Models are ranked according to increasing AICc values. For all raptors, lowest AIC = 3421.65, for Brahminy Kites, AIC = 2397.66, and for Philippine Serpent Eagles, AIC = 1503.08.

Model	*ΔAICc*	*AICc Weights*
All raptors		
$r_{constant}$ $\lambda_{constant}$	0	0.45
r_{time} $\lambda_{constant}$	0.72	0.31
$r_{constant}$ λ_{time}	1.69	0.19
r_{time} λ_{time}	4.60	0.05
Brahminy Kite		
r_{time} $\lambda_{constant}$	0	0.62
$r_{constant}$ λ_{time}	1.68	0.27
r_{time} λ_{time}	3.46	0.11
r_{time} $\lambda_{constant}$	13.20	0.00
Philippine Serpent Eagles		
r_{time} $\lambda_{constant}$	0	0.49
$r_{constant}$ λ_{time}	0.51	0.38
$r_{constant}$ $\lambda_{constant}$	3.69	0.08
r_{time} λ_{time}	4.35	0.06

Table 3. Model averaged parameter estimates for models describing detection and occupancy probabilities of Brahminy Kites, Philippine Serpent Eagles and all raptors considered together. Our models estimated the binomial sampling probability that a particular individual is detected (*r*), and the Poisson intensity parameter of occupancy (λ) at each point. Global detection and transect-specific occupancy probability parameters were calculated from *r* and λ. Standard errors are provided.

	Modeled individual parameter estimates					
	2014		*2015*		*2016*	
	Individual detection (r)	*Intensity parameter (λ)*	*Individual detection (r)*	*Intensity parameter (λ)*	*Individual detection (r)*	*Intensity parameter (λ)*
All raptors	0.15 (0.02)	12.09 (1.27)	0.16 (0.01)	12.15 (1.06)	0.17 (0.02)	12.17 (1.00)
Brahminy Kite	0.14 (0.02)	5.6 (0.03)	0.13 (0.03)	6.20 (1.38)	0.18 (0.03)	6.35 (1.02)
Philippine Serpent Eagle	0.06 (0.02)	8.50 (2.68)	0.06 (0.02)	8.12 (2.43)	0.05 (0.02)	7.52 (2.78)

	Derived global detection and habitat-specific occupancy parameter estimates					
	2014		*2015*		*2016*	
	Detection probability	*Occupancy probability*	*Detection probability*	*Occupancy probability*	*Detection probability*	*Occupancy probability*
All raptors	0.84 (0.02)	1.00 (<0.001)	0.86 (0.01)	1.00 (<0.001)	0.87 (0.02)	1.00 (<0.001)
Brahminy Kite	0.54 (0.03)	1.00 (0.004)	0.56 (0.03)	1.00 (0.002)	0.68 (0.03)	1.00 (0.002)
Philippine Serpent Eagle	0.40 (0.03)	1.00 (0.001)	0.36 (0.03)	1.00 (0.001)	0.30 (0.03)	1.00 (0.002)

Table 4. Study site-specific modeled estimates of numbers of Brahminy Kites, Philippine Serpent Eagles, and all raptors combined. We used the beta coefficients of intensity parameter (λ), and the influence of forest type and level of disturbance to estimate abundance or raptors in each location.

	Estimated abundance or numbers of raptors				
	High elevation montane			*Low elevation dipterocarp*	
	Near-pristine	*Moderately disturbed*	*Severely disturbed*	*Near-pristine*	*Moderately disturbed*
All raptors	16.49	12.84	8.03	13.92	10.83
Brahminy Kite	0.29	0.74	0.36	0.21	0.74
Philippine Serpent eagle	7.60	11.28	4.47	21.09	11.28

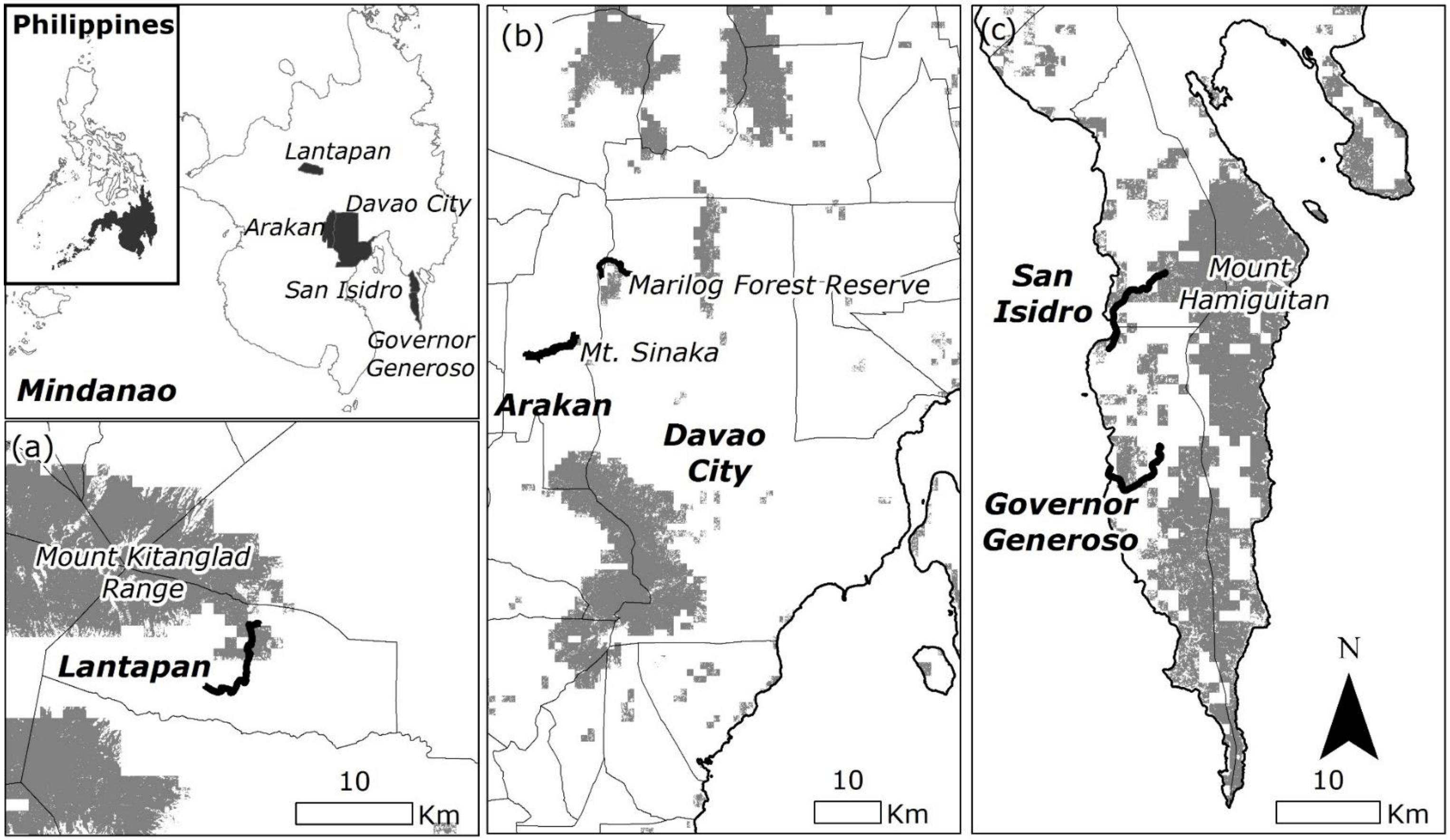

Figure 1. Distribution of areas surveyed around central and eastern Mindanao, Philippines. Inset on the top left shows the entire Philippines; island of Mindanao is shaded. Enlarged map of Mindanao shows the locations of the 5 study areas. Figure part (a) shows the fixed 10-km transect (━) surveyed in Lantapan. Middle map (b) shows the fixed 10-km transect surveyed in Davao City and Arakan. Right map (c) shows the fixed 10-km transect surveyed in San Isidro and Governor Generoso. Areas shaded grey in a, b, and c have at least 50% tree cover and are from Bartholomé and Belward (2005) and Hansen et al (2013). Outlines in a, b and c show town boundaries. Forests nearest to study areas are identified.

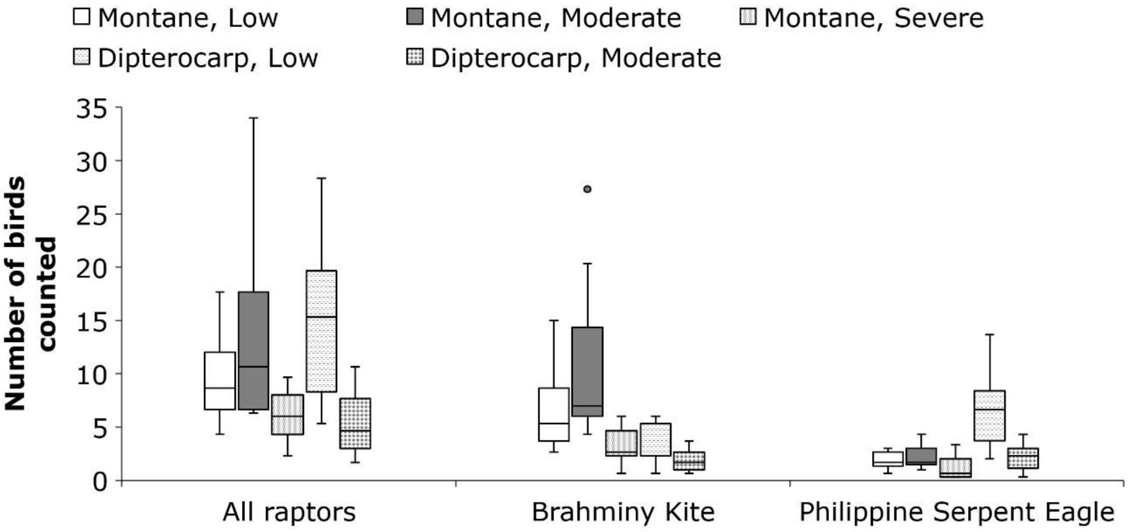

Figure 2. Number of individuals counted of Brahminy Kites, Philippine Serpent Eagles and all raptors combined according to forest type and level of disturbance. Forest type is either high elevation montane or low elevation dipterocarp forest. Level of disturbance is categorized as near-pristine (or low disturbance), moderate or severe.

CHAPTER 5

Modeled island hopping through the Philippines demonstrates trade-offs migrant birds face during oceanic crossings

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SUMMARY

Capsule: Modeling trans-oceanic migration pathways demonstrates that birds face trade-offs among use of stopover sites, duration of over-water travel, and wind direction, and generates testable hypotheses for future study.

Aims: We evaluated the potential migratory responses of "oceanic", island-hopping Grey-faced Buzzards that encounter variation in landscape parameters and weather as they move through and out of the Philippine archipelago.

Methods: We created spatial models and constrained the modeled routes to enter the Philippine island chain at a single northern island, Batan, and to use one of 4 potential exits in the south, either Balabac Island, Bongao Island, Balut Island, or Cape San Agustin on Mindanao Island. We included costs of all possible combinations of our three external parameters (stopover sites, water and wind direction) to model alternative migratory routes for each of the four exit points (n = 20 migratory routes) and we validated modeled routes with published migration data.

Results: Modeled Grey-faced Buzzard migration routes were between 1,582 and 2,970 km and all repeatedly crossed water. Routes overlapped over eastern and central Luzon, along a leading line created by the Sierra Madre Mountains and at long and unavoidable over-water crossings between the islands of Mindoro and Palawan, Negros and Zamboanga del Norte, and Leyte and Mindanao. Observational data were closer than random points to modeled routes for two of the four possible exit points.

Conclusion: Our models suggest that the optimal migratory strategy for these birds is to find the shortest route to an exit point with the greatest possible access to stopover habitats and fewest open-water crossings under wind resistance. Understanding how each of the external factors affected the geography and characteristics of the migratory routes generates testable hypotheses to evaluate strategies of birds that face dangerous open-water crossings on migration.

INTRODUCTION

Migration can be a costly period that can influence regulation of bird populations through its consequences to survival and, in some cases, to reproduction (Newton 1998, 2004). Survival is lower during migration than during non-migratory periods (Sillett and Holmes 2002, Klaassen et al. 2014) and may vary by sex (Sillett and Holmes 2002) or age (Oppel et al. 2015). The consequences of low survival and individual decisions made during migration and wintering in turn have important carry over effects on sex ratio dynamics and reproductive success (Sillett et al. 2000, Norris et al. 2004, Norris and Marra 2007, Dale and Leonard 2011). These effects of migration often are influenced by the range of external conditions that migrants encounter as they move back and forth between breeding grounds and wintering grounds (Runge and Marra 2005, Newton 2006).

To account for these consequences, there is selective pressure to minimize costs associated with energy, time and risk on migration (Alerstam and Hedenström 1998, Henningsson and Alerstam 2005). For example, although migration influences the energy balance of birds (Tucker 1975, Alerstam et al. 2003), migrating raptors are able to reduce energetic costs by using soaring flight (Bildstein 2006). Soaring is fast (Duerr et al. 2012) and so energy efficient (Mandel et al. 2008) that soaring migrants can cover long distances with little or no need to refuel (Kerlinger 1989, Bildstein 2006).

Although soaring can help minimize energy and time, it does not however, reduce safety costs, or risks, associated with over-water travel. When making over-water crossings, the odds of success are much higher when weather conditions are favorable (Meyer et al. 2000, Liechti 2006). Decision lapses over-water are highly consequential because they may lead to fatigue and ultimately death (Bildstein et al. 2009, Oppel et al. 2015). Decision lapses also are especially common for young, inexperienced birds who are still honing navigation and orientation abilities (Thorup et al. 2003, Agostini 2004) and learning appropriate migratory responses to weather and the landscape they encounter (Fagan et al. 2013, Harel et al. 2016). As such, if young, inexperienced birds survive their first over-water crossings, they sometimes do so in spite of being blown off course by wind drift (Thorup et al. 2003, Agostini 2004), and following longer migration routes over extended migration periods (Mellone et al. 2011, Crysler et al. 2016). Despite these challenges, over-water routes are often shorter and, with the assistance of supporting winds and appropriate soaring conditions (Alerstam 1979, Meyer et al. 2000, 2003), may be a significant ecological corridor for birds adapted for such flight (Gill et al. 2009, López-López et al. 2010).

The Grey-faced Buzzard, *Butastur indicus*, regularly completes long-distance, over-water travel and is considered to be one of the most "oceanic" of raptor migrants (Bildstein 2006). Every year, more than 10,000 Grey-faced Buzzards migrate across Taiwan before crossing at least 180 km of open ocean to reach the Philippines (Lin and Severinghaus 1998). Once within the Philippine Archipelago, nearly all of them make multiple, short oceanic crossings while island-hopping through the country. Although some of them over-winter in the Philippines, others make another large ocean crossing, from the southern extent of the archipelago on Palawan and Mindanao to Borneo and Indonesia, 120 km further south (Ferguson-Lees and Christie 2001). Because their migration is both so oceanic and so observable at these few points of land arrival and departure, this species is a good model for understanding the causes and consequences of migration behavior over large expanses of water.

We built spatial models to assess costs, consequences and potential migratory responses of Grey-faced Buzzards to different external factors (e.g. weather conditions and landscape characteristics) and to provide insight into migratory strategies individuals may select along this East Asian Oceanic Flyway. Our models addressed two specific research questions: (a) how may autumn migration routes vary as a result of trade-offs in migratory response; and (b) how the choice of migration strategy may influence which potential exit points would be used as buzzards depart from the Philippines. We then interpret these outputs to provide insight into the relative costs and benefits to each migratory strategy and to other migrants that also make substantial ocean crossings.

METHODS

Study area

The Philippines is a tropical, southeast Asian archipelago made up of over 7,000 islands with a land area of 300,000 km^2 (Fig. 1). Land cover is a mosaic of rainforests, croplands and plantations (Catibog-Sinha and Heaney 2006). The forests that have not been cleared for agriculture (i.e. lowland dipterocarp, high elevation montane, and mangroves) are found mostly in the northern and southern parts of the island of Luzon, and on the islands of Palawan and Mindanao. Natural grasslands have been converted primarily for agriculture and agro-forestry.

The Philippines belongs to the "Maritime Continent" (Ramage 1968) and experiences a monsoon-type climate, with high temperatures, high humidity and abundant rainfall throughout the year (Chang et al. 2004, Saha 2010). Mean annual temperature across the country is 25—28°C. Average rainfall is between 1—4 m annually. The southwest monsoon and northeast monsoon alternate through the region in a seasonal cycle. From May to September, the southwest monsoon brings hot and humid weather and frequent rainfall as a result of warm, moist air (PIDS 2005, Saha 2010). This southwest monsoon brings rains to the western side of the Philippines. From October to late March, the northeast monsoon, dominated by trade winds, brings moderate temperatures and little or no rainfall as a result of cool winds. These minor northeast monsoon rains affect the eastern side of the Philippines. The Philippines also experiences cold fronts from November to February which increase cloudiness and can produce heavy rains nationwide.

Focal species

The Grey-faced Buzzard is a small raptor that breeds in eastern-mainland Asia and winters in southern East Asia and parts of Pacific Asia (Ferguson-Lees and Christie 2001). Some Grey-faced Buzzards migrate to and winter in the Philippines whereas others migrate through and continue on to more southerly destinations. Grey-faced Buzzards are believed to exhibit high fidelity to both migration routes and to stopover sites (Shiu et al. 2006). The species' passage has been suggested as a good indicator to identify important raptor migration watchsites (Lin and Severinghaus 1998).

The Grey-faced Buzzard occupies open habitat (Gamauf et al. 1998, Sakai et al. 2011), favoring farmlands sharing edges with forests or wooded areas (Matsuura et al. 2005, Wu et al. 2006). Although it may use a wide range of farmlands, the Grey-faced Buzzard prefers to forage for frogs, lizards and grasshoppers in cultivated or wet rice paddy fields during both breeding and wintering season (Momose et al. 2005, Kadowaki et al. 2007, Sakai et al. 2011). The wintering home range of Grey-faced Buzzards is 0.25 to 0.75 km^2 (Wu et al. 2006). Conversion of agricultural lands, particularly the abandonment of rice paddy fields, has led to a well-documented and rapid decline in Grey-faced Buzzard breeding population in Japan (Kawakami and Higuchi 2003, Ueta et al. 2006a).

Modeling approach

To provide a framework to understand why Grey-faced Buzzards take particular migration routes, we used ArcGIS 10.2.2 (ESRI 2014) to create deterministic models of Grey-faced Buzzard autumn migratory routes across the Philippines. We completed this in three stages. First, we evaluated the “cost” of movement as a result of landscape features (i.e., costs induced by distances between stopover sites on land and costs induced by over-water travel) and weather conditions (i.e. costs induced by changes in wind direction) buzzards encounter as they migrate through the archipelago. These calculations were based on model input data and cost estimates described below.

Second, we used accumulated cost surface methods (the value of a grid cell represents the combined energetic and safety cost of moving from that grid cell to an exit point; Eastman 1989, Douglas 1994, Collischonn and Pilar 2000) to determine likely routes buzzards use to reach logical exit points in the south of the country. The four exit points we used were Balabac Island, Bongao Island, Balut Island, and Cape San Agustin on Mindanao Island (Fig. 1). Each of these exit points are at a southernmost island tip and each is the closest point to either the island of

Borneo (shared by the countries of Malaysia, Brunei and Indonesia) or other Indonesian islands. Finally, we evaluated characteristics of these potential movement trajectories to determine the shortest and least costly routes buzzards could follow to move from the northernmost tip of the Philippines (Batan Island) to each exit point.

We used 1-km resolution as the standard processing cell size for our models. Because this is close to the known winter home range size of the species, we assumed that this would reasonably represent the scale at which Grey-faced Buzzards use the landscape, especially during stopovers. We transformed all maps from a geographic coordinate system (WGS 1984) to a projected coordinate system (WGS 1984 UTM Zone 51N).

Model input data

We used land cover and climate data for Philippine terrestrial habitat and all surrounding marine habitat that were within 4°N (southernmost extent of latitude) to 22°N (northernmost latitude), and 116°E (westernmost longitude) to 128°E (easternmost longitude). Data sources are described below; all maps were scaled or resampled to a 1-km grid cell size for modeling. Our Philippine boundary map was downloaded from the Global Administrative Areas website (GADM 2011).

To describe land cover types that buzzards might encounter on migration, we used the Global Land Cover (GLC) 2000 dataset which classified land cover in 17 categories (GLC 2003). Because Grey-faced Buzzards are known to use rice paddies as foraging habitat, we supplemented land cover data with a 'percent of rice planted in an area' dataset (Ellis et al. 2010).

To identify potential migration stopover sites for Grey-faced Buzzards, we followed a two-step process. First, we used ArcGIS to create binary maps for habitat type. Our binary map for rice fields identified all 1 km grid cells with rice fields as 1, and all grid cells with other habitats as 0. Similarly, our binary map for wooded areas identified all grid cells with closed-canopy forests, open-canopy forests or plantations as 1, and all grid cells with other habitats as 0.

We then used the 'Extract raster edge' tool of the Geospatial Modelling Environment (Beyer 2012) to identify rice fields adjacent to wooded areas, thought to be critical habitats for Grey-faced Buzzards (Kawakami and Higuchi 2003, Ueta et al. 2006b). We selected these areas because previous work (eg. Matsuura et al. 2005, Momose et al. 2005, Wu et al. 2006) suggests that each 'edge' could be used as a stopover site. We identified 60,442 km^2 of rice fields and 79,250 km^2 of wooded areas resulting in 6,567 potential 1- km^2 stopover sites across the Philippines. Of these, 2,887 are in Luzon, 1,111 in the Visayas and 2,569 in Mindanao.

To identify areas that would involve over-water travel, we created a binary map identifying all grid cells of water bodies as 1, and all landforms as 0. To describe weather that buzzards may encounter on migration, we used wind data measured at 50 m above the surface of the earth from the month of October (the primary month of buzzard migration) and averaged over 22 years (1983—2005) (Stackhouse Jr. 2013).

Calculating movement costs

To evaluate the cost of moving between stopover sites, we computed the straight-line (Euclidian) distance between any given cell to the nearest 1- km^2 potential stopover site. In the resulting stopover distance cost map, each 1- km^2 cell had a stopover distance cost value ranging from 0 to 547 km, with mean 130 km (SD = 121 km).

To evaluate the cost of moving in winds of different directions, we reclassified wind direction to make traveling in winds blowing from the north (tailwinds, 135°—225°) 1.08x less costly than moving in crosswinds blowing from the northeast or the northwest (crossing tailwinds, 90°—135° and 225°—270°) and 1.20x less costly than moving in crosswinds blowing from the southeast or southwest (crossing headwinds, 45°—90°). Thus, each km traveled with crossing tailwinds was equivalent to traveling 1.08 km with tailwinds and each km traveled with crossing headwinds was equivalent to traveling 1.2 km with tailwinds. These hypothetical costs were based on estimates derived from wandering albatross (*Diomedea* *exulans*) heart rates when flying in different wind directions (Weimerskirch et al. 2000). To our knowledge no similar data exist for Grey-faced Buzzards or for any other similarly behaving raptors of any type. In this analysis, costs over land and water are considered to be similar.

The cost of over-water travel for a soaring migrant like the Grey-faced Buzzard is low when wind conditions are favorable (i.e., with tailwinds; Meyer et al. 2000, Liechti 2006, Panuccio et al. 2016). Under crosswinds or headwinds however, the safety costs increase to the point that birds may alter their route to avoid water crossing or to reduce time spent under unfavorable wind conditions (Bildstein et al. 2009, Nourani et al. 2016). To incorporate costs of water crossings with a crosswind or headwind, we reclassified our water dataset so that Grey-faced Buzzards would never travel over-water under crosswinds or headwinds. Thus, each km traveled over water under tailwind was equivalent to traveling 1 km over land under tailwind. Cost of traveling with a crossing tailwind over land was equivalent to traveling 1.08 km with tailwinds over land. The cost of traveling into a crossing headwind over land was equivalent to traveling 1.2 km with tailwinds over land.

Determining movement possibilities and optimum paths

To evaluate the potential costs and benefits of different buzzard migration routes, we calculated the effective distance (accumulated travel cost) of all possible paths from an exit point to every grid cell. We used the 'Cost distance' tool in ArcGIS and assigned an exit point (the "source data" in the cost distance tool) and a gridded cost dataset (see below; the "cost raster" in the cost distance tool). Accumulated travel costs were stored in a cost distance dataset and a direction dataset.

To determine the optimum paths, we identified the paths with the shortest effective distance (least-costly) linking an exit point to the entry point. We used the 'Cost path' tool in ArcGIS and assigned the buzzard's starting point (Batan; the "destination data" in the cost path tool) and the accumulated travel costs (the outputs from the cost distance tool; the "cost distance raster" in the cost path tool). The GIS then calculates an "optimum path" which is the least costly route relative to the exit point and to the cost dataset (the two inputs into the cost distance tool). The cumulative route cost is unitless and thus is directly comparable among different exit points that used the same gridded cost dataset. However, these route costs are not useful for comparing alternatives when gridded cost datasets are not identical.

To understand how routes may vary as a result of trade-offs buzzards face (research question #1), we prepared different gridded cost datasets based on all possible combinations of our 3 parameters (n = 20 migratory routes). We combined cost datasets by multiplying them. We could not consider over-water costs without incorporating winds and models that required over-water costs only were not considered. Our gridded cost datasets were based on the following:

- Cost of moving between stopover sites only (n = 4 migratory routes, one to each endpoint)
- Cost of wind direction only (n = 4 migratory routes)
- Combined costs of stopover distances and wind direction ([Stopover distances * Wind costs], n = 4 migratory routes)
- Combined costs of wind direction and over-water travel ([Wind costs * Over-water costs], n = 4 migratory routes)
- Combined costs of stopover distances, over-water travel and wind direction ([Wind costs * Over-water costs * Stopover distances], full model, n = 4 migratory routes)

We used descriptive statistics to evaluate the different characteristics (route length, distance between stopovers, over-water length, length with specific wind directions) of our 20 migratory routes. As a sensitivity analysis, we compared distance traveled (total distance, distance between stopovers, distance over water, distance with specific wind directions) when we varied the cost datasets used in the model. Finally, within each of the five alternatives above, we compared movement costs (unitless), to determine which exit point we expected would be used depending on the migration strategy the buzzards used (research question #2).

Movement cost is a better measure than distance traveled because it also captures energetic and safety costs along each route (Etherington and Holland 2013).

Validation

To check the viability of our modeled routes, we compared our modeled migration routes to published (McClure 1974, 1998) citizen-science (eBird 2012, Wild Bird Club of the Philippines 2015), and personal (CBC unpublished data) observations of Grey-faced Buzzards during migration season (n = 29 individual observations, Fig. 3). We assumed that if our migration routes reasonably represent buzzard migration, then observations of buzzards should be located closer to modeled migration routes than would random points. To test this assumption, we created a distribution map of the 29 “observation points” and 87 random points. We used the ‘Near’ tool in ArcGIS to determine the distance of each of our observation and random points to each of our modeled route and we used a Mann-Whitney U-test to compare, for each of the 20 routes, distances from routes to observation and random points.

To test the effectiveness of the routes modeled for each of the 4 exit points, we used a Kruskal Wallis test with a Nemenyi test for post-hoc analyses (Nemenyi 1969) to compare the average difference in observed and random point-to-route distances according to exit point. Finally, we used a Kruskal Wallis test to test the effectiveness of each of the 5 cost datasets used in modeling our routes by comparing observed and random point-to-route distances according to cost dataset. All statistical analyses were conducted with R statistical software, using the ‘stats’ package (lm, wilcox.test, kruskal.test,) and ‘PMCMR’ package (posthoc.kruskal.nemenyi.test) (R Development Core Team 2013).

RESULTS

Route variation and trade-offs in migratory response

Our 20 modeled routes reflect the consequences of a hypothetical buzzard’s migratory response to external parameters. These routes varied depending on the strategy a buzzard might choose as it moves through the Philippines (Table 1, Fig. 2).

The modeled routes were between 1,582 and 2,970 km in length ($\bar{x}$ = 2,176, SD = 373). There were between 0 and 282 stopovers ($\bar{x}$ = 140, SD = 112) on every route. On routes with more than one stopover, the distance between stopovers ranged from 40 to 899 km ($\bar{x}$ = 159, SD = 201). Over-water crossings accounted for 11 to 99% ($\bar{x}$ = 33%, SD = 26%) of the total route length. Tailwinds were only present along some of the routes leading to Balabac and Bongao and occurred on 0 to 28% ($\bar{x}$ = 7%, SD = 9%) of the route length. Tailwinds were not encountered along any of the routes leading to Balut Island and Cape San Agustin. Crossing tailwinds were encountered along 38 to 93% ($\bar{x}$ = 53%, SD = 12%) of the total route lengths, while crossing headwinds were encountered along 7 to 61% ($\bar{x}$ =43%, SD = 12%) of the route lengths.

If a modeled Grey-faced Buzzard was migrating to Balabac, it would always follow a route along eastern Philippines. However, if a modeled buzzard was migrating to Bongao, Balut Island or Cape San Agustin, it would either travel along a western route or an eastern route.

Single-parameter models. A hypothetical Grey-faced Buzzard that tries to minimize distances between stopover sites to reach any of the logical exit points (Fig. 2A) will travel along migratory routes that are up to 37% longer ($\bar{x}$ = 30% difference, SD = 7%) than the route of a buzzard minimizing only wind resistance (Fig. 2B). However, such a buzzard will travel shorter distances between stopover sites ($\bar{x}$ = 159% fewer kilometers, SD = 7%) than a buzzard responding only to wind resistance. The most likely routes of travel for a buzzard minimizing distances between stopover sites to reach either Bongao, Balut Island or Cape San Agustin would involve travel along the western side of the country.

A hypothetical buzzard that tries to minimize wind resistance to reach any of the logical exit points (Fig. 2B) will move along 'straighter' and shorter routes than a buzzard minimizing only stopover distances. Such a buzzard will travel along migratory routes with longer over-water crossings ($\bar{x}$ = 111%, SD = 9%) than a buzzard responding only to stopover distances. A buzzard minimizing wind resistance to reach Balabac will not have any access to stopover sites. A buzzard minimizing wind resistance to reach either Balabac or Bongao would receive more wind assistance from tailwinds than a buzzard heading towards any other exit point.

Multiple-parameter models. A hypothetical Grey-faced Buzzard that attempts to minimize both distances between stopover sites and wind resistance to reach any of the logical exit points (Fig. 2C) will travel along migratory routes that are up to 29% longer ($\bar{x}$ = 17%, SD = 9%) than would a buzzard minimizing both wind resistance and over-water travel (Fig. 2D). Such a buzzard would travel shorter distances between stopover sites ($\bar{x}$ = 172%, SD = 4%) and encounter less resistance from northward crosswinds ($\bar{x}$ = 23%, SD = 17%) than would a buzzard responding to both wind resistance and over-water travel. A buzzard minimizing both stopover distances and wind resistance to reach Bongao would receive more wind assistance from tailwinds than a buzzard heading towards any other exit point. A buzzard minimizing both stopover distances and wind resistance to reach either Bongao, Balut Island or Cape San Agustin would most likely migrate along the western part of the country.

A hypothetical buzzard that attempts to minimize both wind resistance and over-water travel (Fig. 2D) will travel along straighter and shorter routes than a buzzard minimizing both stopover distances and wind resistance. Such a buzzard would travel along migratory routes with shorter over-water crossings ($\bar{x}$ = 32%, SD = 12%) than a buzzard responding to both stopover distances and wind resistance. A buzzard minimizing both stopover distances and wind resistance to reach Bongao would receive more wind assistance from tailwinds than a buzzard heading towards any other exit point. A buzzard minimizing both stopover distances and wind resistance to reach either Bongao, Balut Island or Cape San Agustin would migrate along the eastern side of the country.

A hypothetical buzzard that responds to minimizing stopover distances, over-water travel and wind resistance (Fig. 2E) will travel along routes that are up to 16% shorter ($\bar{x}$ = 8%, SD = 5%) than the route of a buzzard minimizing both stopover distances and wind resistance (Fig. 2C) and routes that are up to 23% longer ($\bar{x}$ = 21%, SD = 2%) than the route of a buzzard minimizing both wind resistance and over-water travel (Fig. 2D). Such a buzzard will travel longer distances between stopover sites ($\bar{x}$ = 11%, SD = 8%) than a buzzard responding to stopover distances and wind resistance and travel shorter distances between stopover sites ($\bar{x}$ = 101%, SD = 32%) than a buzzard responding to wind resistance and over-water travel. Such a buzzard will take shorter over-water crossings ($\bar{x}$ = 37%, SD = 18%) and encounter more resistance from crossing headwinds over land ($\bar{x}$ = 13%, SD = 16%) than a buzzard responding to any other combination of parameters. A buzzard minimizing stopover distances, wind resistance and over-water travel to reach Bongao would receive more wind assistance from tailwinds than a buzzard heading towards any other exit point. A buzzard minimizing stopover distances, wind resistance and over-water travel to reach either Bongao, Balut Island or Cape San Agustin would migrate along the eastern side of the country.

Possible autumn migratory routes and movement funnels

To identify how destinations influenced movement costs, we identified the least costly (in terms of movement costs) route alternatives from each of our gridded cost datasets. In each case, these comparisons were for each of the five sets of conditions laid out in the methods; this method does not allow us to compare costs from models that started with different cost datasets. One of our least costly routes led to Balabac (Wind costs only, Fig. 3B), two led to Balut Island (Stopover distances only, Fig. 3A; and Stopover distances * Wind costs, Fig. 3C), and two led to Cape San Agustin (Wind costs * Over-water costs, Fig. 3D; and Wind costs * Over-water costs * Stopover distances, Fig. 3E).

We identified areas where our modeled routes overlapped or suggested relatively long and unavoidable over-water crossings. Sixteen out of our 20 modeled routes passed over eastern and central Luzon, along a leading line created by the Sierra

Madre Mountains, the longest mountain range in the country (Fig. 1.A). At the southwest of Luzon, there is an unavoidable 70 km over-water crossing between Mindoro and Palawan (Fig. 1.B). Birds migrating to Palawan or exiting the country through Balabac would feed through this bottleneck. This crossing was in four of five routes leading to Balabac. At the southwest of the Philippines, there is a 50 km bottleneck over water between the islands of Negros and Zamboanga del Norte (Fig. 1.C). Birds wintering in Mindanao, or continuing on to presumed destinations in Borneo and Indonesia through Bongao, Balut Island or Cape San Agustin would encounter this water crossing. To reach this particular bottleneck, buzzards would have to island hop across western Visayas, involving over-water crossings ranging from 9 to 50 km. This funnel was in 7 of the 15 modeled routes for Bongao, Balut Island and Cape San Agustin. Finally, at the southeast of the Philippines, there is an unavoidable 20 km over-water crossing between Leyte and Surigao (Fig. 1.D). Birds wintering in Mindanao, or continuing on to presumed destinations in Indonesia through Bongao, Balut Island or Cape San Agustin would be forced through this bottleneck. This water crossing was in six of the modeled routes leading to Bongao, Balut and Cape San Agustin.

Model validation

Observation points and random points were not randomly distributed with regards to five routes modeled for the four exit points (Kruskal-Wallis, $\chi2 = 16.303$, df = 3, p = 0.001). Post hoc tests showed that observation points were closer than random points to the modeled routes leading to Balut and Cape San Agustin than to routes leading to Balabac and Bongao (Fig. 4). In addition, observation points were significantly closer than random points to two out of five modeled routes leading to Cape San Agustin (Table 2). Observation points and random points had similar distances to route alternatives (one for each exit point) modeled according to our five gridded cost datasets (Kruskal-Wallis, $\chi2 = 0.3286$, df = 6, p = 0.9879).

DISCUSSION

The spatial models we built assessed costs, consequences and potential migratory responses by Grey-faced Buzzards to external factors and provided insight into migratory strategies individual birds may select. These models showed how migratory routes may vary as calculations for movement costs and targeted exit points changed, Finally, they provide insight into trade-offs in migratory responses, potential exit points used according to migration strategy, and potential optimal migration strategies of buzzards and other birds facing open-water crossings.

Trade-offs in migratory response

Our spatial models describe possible variation in migratory routes used by Grey-faced Buzzards moving across the Philippine archipelago in response to landscape parameters (stopover sites and water crossings) and weather conditions (wind direction). These modeled routes allow us to examine the costs and consequences of different migratory responses in the case when migrants have to repeatedly decide between completing, delaying or foregoing over-water travel.

The general direction in which birds fly is believed to be either genetically inherited or culturally learned (Berthold et al. 1992, Sutherland 1998, Gschweng et al. 2008). Avian migratory routes are then adjusted by each individual through continual assessment and reassessment of habitat and other factors they encounter (Hutto 1985, Vardanis et al. 2011). The ideal migratory route is thought to be one that minimizes the costs of migration, as measured in terms of combinations of energy, time, or risk (Hedenström and Alerstam 1997, Liechti and Bruderer 1998, Alerstam et al. 2003, Alerstam 2011). The resulting characteristics of these routes thus reflect the bird's assessment of the potential costs and benefits of each route over time (Hutto 1985).

In our models of migration through the Philippines, the cost of movement between potential stopover sites was the factor that had the most influence on the characteristics of the autumn migratory routes of Grey-faced Buzzards. In response to availability of stopover sites, a hypothetical buzzard not only shortened distances traveled between stopovers, it also had potential access to more stopover sites than would a buzzard following a different strategy. However, responding to stopovers resulted in migratory routes that were longer and more tortuous (less straight) than necessary (Hake et al. 2003, Thorup et al. 2003, González-Solís et al. 2009). For a buzzard behaving in this manner, an optimal migratory route therefore may be one that first maximizes opportunity for stopovers and secondarily minimizes distance traveled. The importance of stopover sites corresponds well with the known biology of the species. In fact, stopover sites have been found to be important to Grey-faced Buzzard migratory routes and buzzards exhibit high fidelity to some of these sites (Shiu et al. 2006).

As Grey-faced Buzzards migrate, they complete long-distance, over-water travel (Bildstein 2006). However, after Grey-faced Buzzards enter the Philippine archipelago, they may still tend to select routes with fewer and shorter over-water crossings whenever possible (Bildstein 2006, Shiu et al. 2006). Often, there are limited options to minimizing the safety costs of over-water travel (i.e., there is only one point in an island with the narrowest water crossing) and the routes of individual buzzards will geographically converge around a common, population-level route (La Sorte et al. 2016). This makes unavoidable over-water crossings, such as those suggested between Mindoro and Palawan, Negros and Zamboanga del Norte and Leyte and Surigao, potentially important funnel points for Grey-faced Buzzard migration.

In our models of migration through the Philippines, minimizing the risks involved with over-water travel altered the geography or location of migratory routes. When trying to minimize over-water crossings, a hypothetical buzzard would travel through an eastern route to reach either Bongao, Balut Island or Cape San Agustin. A buzzard who does not respond to risk associated with over-water crossings would travel a western route to reach either of these three exit points. This is because eastern routes had greater distances with unfavorable, crossing headwinds over land than did a western route. This illustrates the broadly-based trade-offs migrants face in favoring minimizing the risks of traveling over-water under wind resistance over minimizing the energetic costs associated with unfavorable winds over land.

Finally, in our models of migration through the Philippines, minimizing the costs of wind resistance had the weakest influence on both the characteristics and geography of migratory routes. If minimizing wind resistance is the only goal, a hypothetical buzzard would travel a short and straight route. A buzzard flying along this low-cost migratory route would have limited access to key resources and face repeated open-water crossings.

Exit points according to migration strategy

The migration strategy of a hypothetical buzzard would influence the exit point from which it departs the Philippines. Based on our model of migration through the Philippines, Balabac would be the most likely exit point for a buzzard that minimizes island hopping and wind resistance. Such a buzzard will have little to no opportunity for stopovers but will also migrate less distance from its entry point at Batan. A buzzard who began migration later in the season and feels pressure to minimize migration time may be most likely to behave this way. Although autumn migration has not yet been directly studied at Balabac, autumn migrants have been observed from research vessels traveling over the South China Sea between Balabac and Borneo (Simpson 1983, Ellis et al. 1990).

Our models suggest that Bongao is the least likely exit point used during autumn regardless of a buzzard's migration strategy. In fact, this prediction corresponds well with known migration patterns through Bongao. For example, telemetered Oriental Honey-buzzards Pernis ptilorhyncus that winter in the Philippines are known to use Bongao as an entry point into the country during autumn migration and an exit point from the country during spring (Higuchi et al. 2005, Yamaguchi et al. 2008). However, no tracked honey-buzzards have used Bongao as an exit point in autumn.

Based on our models of migration through the Philippines, Balut Island is the most likely exit point for a buzzard that minimizes distances traveled between stopover sites and minimizes wind resistance. Such a buzzard would maximize opportunities for stopovers along a western route where wind resistance is less prevalent. A buzzard aiming to save energy in migration might behave this way as the wind conditions of a western route may facilitate migration. Autumn migration has not yet been directly studied at Balut Island although raptor migrants have been monitored about 20 km northwest of Balut Island (Tiongco et al. 2014) and in Sulawesi, Indonesia, almost 200 km south (Germi et al. 2009).

Finally, Cape San Agustin is the most likely exit point for a buzzard that minimizes distances traveled between stopover sites, minimizes wind resistance, and minimizes over-water crossings. Such a buzzard will maximize opportunities for stopovers along an eastern route where there are few over-water crossings between islands despite great wind resistance over land. A buzzard aiming to minimize risks from over-water travel might behave this way. There is evidence that this strategy is used and raptor migrants have been directly observed initiating autumn ocean crossings from Cape San Agustin, heading towards the direction of Sulawesi-Talaud (Indonesia) (Concepcion et al. 2017).

Optimal migration strategy

Field data supported our models better when routes were evaluated according to the exit point than when evaluated according to costs of movement. Although the rate of correspondence between these field data and modeled data was not strong, this is not unexpected given the nature of the field data available (there are no systematic studies of this problem and only a few anecdotal observations are reported in literature). Our modeled routes are similar to migration routes for a similarly sized Accipiter using the same flyway. Nevertheless, the two exit points that our models predict would be most used (Balut Island and Cape San Agustin) had the best correspondence to the validation data and are likely the most used routes by migrating raptors.

Examining specific migratory responses to each external factor allowed us to identify possible optimal migration strategies for Grey-faced Buzzards when navigating oceanic flyways through archipelagos. Our models suggest that the optimal migratory strategy for these birds is to find the shortest route to an exit point with the greatest possible access to stopover habitats and fewest open-water crossings under wind resistance. Therefore, an optimally migrating bird might not necessarily use the straightest and shortest routes (i.e., the modeled routes produced using only the cost of wind direction). In fact, these straightest and shortest routes seem unlikely pathways for experienced migrants. If experienced buzzards indeed maximize refueling opportunities at stopovers and minimize risks through fewer over-water crossings under wind resistance, they may generally be energy-minimizers during autumn migration across the Philippines. This hypothesis could be tested in two ways, one by evaluating if older, more experienced migrants indeed choose these routes, or two, by using telemetry to evaluate if birds conform more consistently with these modeled predictions as they gain experience.

Optimal migration strategies may vary by season. For example, if island crossings and wind conditions have a strong influence on spring migratory routes, Grey-faced Buzzards may be energy-minimizers during that season as well. In fact, the distribution of favorable winds are drastically different between seasons (Wyrtki and Meyers 1975) and during spring, strong resistance from southward winds would intensify energetic and safety costs of crossing from Indonesian islands to the Philippines. To minimize energy expenditure and risk, migrants would have to avoid the Philippines during spring and fly northward following the East-Asian Continental Flyway. In fact, this is the strategy that Oriental Honey-buzzards use (Yamaguchi et al. 2011, Nourani et al. 2016). Using this route greatly reduces over-water travel and allows migrants to benefit from wind support and convective conditions over land. In contrast, Grey-faced Buzzards may be time minimizers during spring and return along the same route they traveled southbound. By doing this, the birds would expend energy compensating for southward winds but would save migration time by avoiding a huge detour around the South China Sea.

Tracking data of birds captured in Japan and migrating within Japanese islands indicates autumn and spring routes remain similar, although stopover sites used were different (Shiu et al. 2006), suggesting that birds select for time minimization. Migration monitoring at the Indonesia island of Sangihe are similarly supportive of a time minimization hypothesis, revealing migrants regularly traveling over-water under heavy opposing winds in spring (Germi et al. 2009). Likewise, spring migration counts conducted in the northern coast of Luzon also support this concept of time minimization via reverse migration (Wild Bird Club of the Philippines 2015), although less strongly than would tracking data from the Philippines.

Raptor migration on oceanic flyways in general, through the Philippines in particular, remains poorly understood. Our models of migration through the Philippines were derived from somewhat limited existing natural history information. Although relatively low in complexity, they allow us to better understand the potential trade-offs between the costs and consequences of migratory responses to landscape and weather conditions along an oceanic flyway. They also serve as an important foundation by producing specific and testable hypotheses about the evolution of this behavior in general and, specifically to the Philippines, locations of potentially good count sites, about potential migration tracks of these birds, and about the distribution of exit points birds may use as they migrate across the Philippines.

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Table 1. Characteristics of 20 modeled Grey-faced Buzzard autumn migratory routes leading to four logical exit points in the south of the Philippines. These routes were modeled using 5 different cost raster datasets as follows: Stopover distances only; Wind costs only; Stopover distances * Wind costs; Wind costs * Over-water costs; and Wind costs * Over-water costs * Stopover distances. See text for additional details.

	Length (km)	Number of potential stopovers	Average distance between stopovers	Proportion of route over water, %	Wind direction, Proportion of route, %			Movement cost (unitless)
					Tail-wind	Crossing tailwind	Crossing headwind	
Stopover distances								
Balabac	1,923	158	90.17	25	1	58	41	36,615,570
Bongao	2,527	239	90.17	29	15	50	35	49,192,170
Balut	2,408	270	39.90	21	0	64	36	33,832,480
Cape San Agustin	2,536	282	42.19	20	0	58	42	34,255,860
Wind costs								
Balabac	1,582	0	—	99	0	93	7	1,730
Bongao	1,798	1	898.95	83	28	38	34	1,945
Balut	1,810	15	279.65	74	0	52	48	2,043
Cape San Agustin	1,750	3	437.45	77	0	47	53	1,988
Stopover distances * Wind costs								
Balabac	1,923	154	41.68	25	1	58	41	39,960
Bongao	2,527	243	87.32	29	15	50	35	52,390
Balut	2,410	270	39.90	21	0	63	37	37,056
Cape San Agustin	2,535	283	42.06	20	0	58	42	37,544
Wind costs * Over-water costs								
Balabac	1,662	13	191.75	22	0	58	42	477,518
Bongao	2,419	17	152.59	22	15	47	38	478,997
Balut	1,981	24	163.75	13	0	43	57	428,461
Cape San Agustin	1,900	18	198.87	13	0	40	60	412,047

	Length (km)	Number of potential stopovers	Average distance between stopovers	Proportion of route over water, %	Wind direction, Proportion of route, %			Movement cost (unitless)
					Tail-wind	Crossing tailwind	Crossing headwind	
Wind costs * Over-water costs * Stopover distances								
Balabac	2,011	158	47.08	18	1	56	43	28,870,950
Bongao	2,970	223	91.82	17	13	48	39	27,677,460
Balut	2,506	223	50.89	11	0	42	58	25,996,470
Cape San Agustin	2,335	211	43.51	11	0	39	61	25,888,830

Table 2. Means and standard deviations (SD) of distance from modeled routes to 29 observations of Grey-faced Buzzards during migration season and to 87 random points. Also shown are results of Mann Whitney U tests to compare distances of observation points and of random points to each of the 20 modeled migratory routes using 5 different cost raster datasets as described in Table 1. Significant *p*-values are bold.

	Observation points		**Random points**		**Mann Whitney U**	
	Mean	**SD**	**Mean**	**SD**	***W***	***p***
Stopover distances						
Balabac	213	304	198	248	1,189	0.6462
Bongao	108	123	104	104	1,202	0.7068
Balut	72	93	105	119	1,013	0.1138
Cape San Agustin	61	94	98	117	921	**0.0302**
Wind costs						
Balabac	387	291	376	244	1,337	0.6325
Bongao	213	218	202	190	1,275	0.9339
Balut	195	107	226	118	1,031	0.1425
Cape San Agustin	172	125	219	129	982	0.0753
Stopover distances * Wind costs						
Balabac	213	304	198	248	1,189	0.6462
Bongao	108	123	104	104	1,202	0.7068
Balut	72	93	105	119	1,013	0.1138
Cape San Agustin	61	94	98	117	921	**0.0302**
Wind costs * Over-water costs						
Balabac	219	304	209	249	1,189	0.6462
Bongao	97	98	93	92	1,276	0.9289
Balut	77	113	110	144	1,001	0.0974
Cape San Agustin	77	112	112	147	981	0.0742
Wind costs * Over-water costs * Stopover distances						
Balabac	200	252	198	250	1,163	0.5321
Bongao	86	102	76	88	1,239	0.8884
Balut	65	109	98	140	956	0.0518
Cape San Agustin	66	108	103	148	955	0.0511

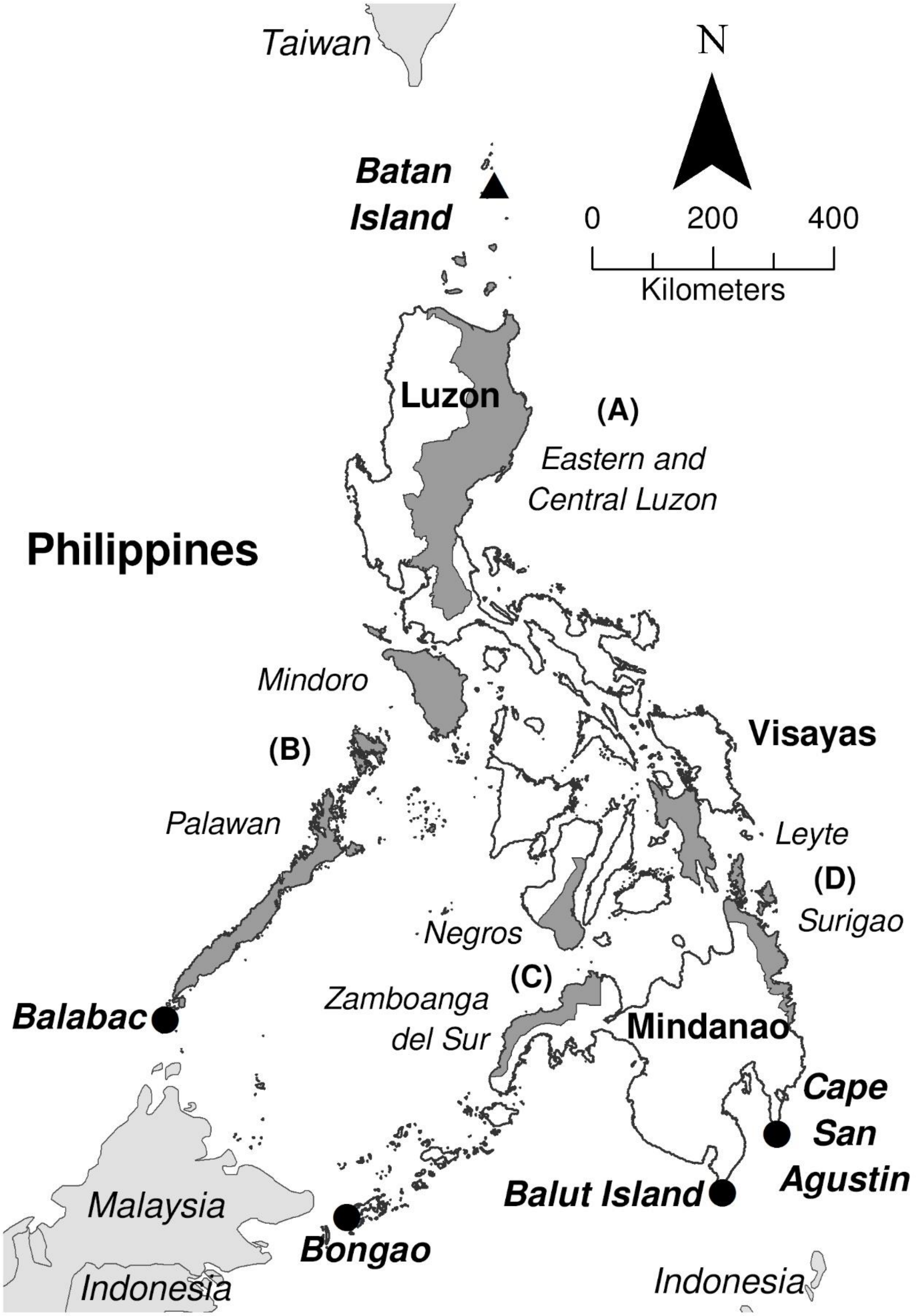

Figure 1. Geographic locations of migratory entry (▲) and exit points (●) in the Philippines. The Philippine archipelago is divided into three island groups: Luzon in the north, Visayas in the middle, and Mindanao in the south. The entry point of

Batan is 180 km south of Taiwan and 280 km north of mainland Luzon. The exit point of Balabac is 70 km north of Borneo, while Bongao is 60 km east of Borneo. Balut Island is 180 km north of Indonesia, while Cape San Agustin is 200 km north. Also shown are four potential migration funnels (shaded gray) that were identified based on modeled Grey-faced Buzzard migratory routes. (A) At eastern and central Luzon, a bottleneck passes along the Sierra Madre Mountains, the longest mountain range in the country. (B) An unavoidable 70 km over-water crossing exists between the islands of Mindoro and Palawan. (C) A bottleneck between the islands of Negros and Zamboanga del Norte includes a 50 km over-water crossing. (D) An unavoidable 20 km over-water crossing exists between the island of Leyte and Surigao on Mindanao Island.

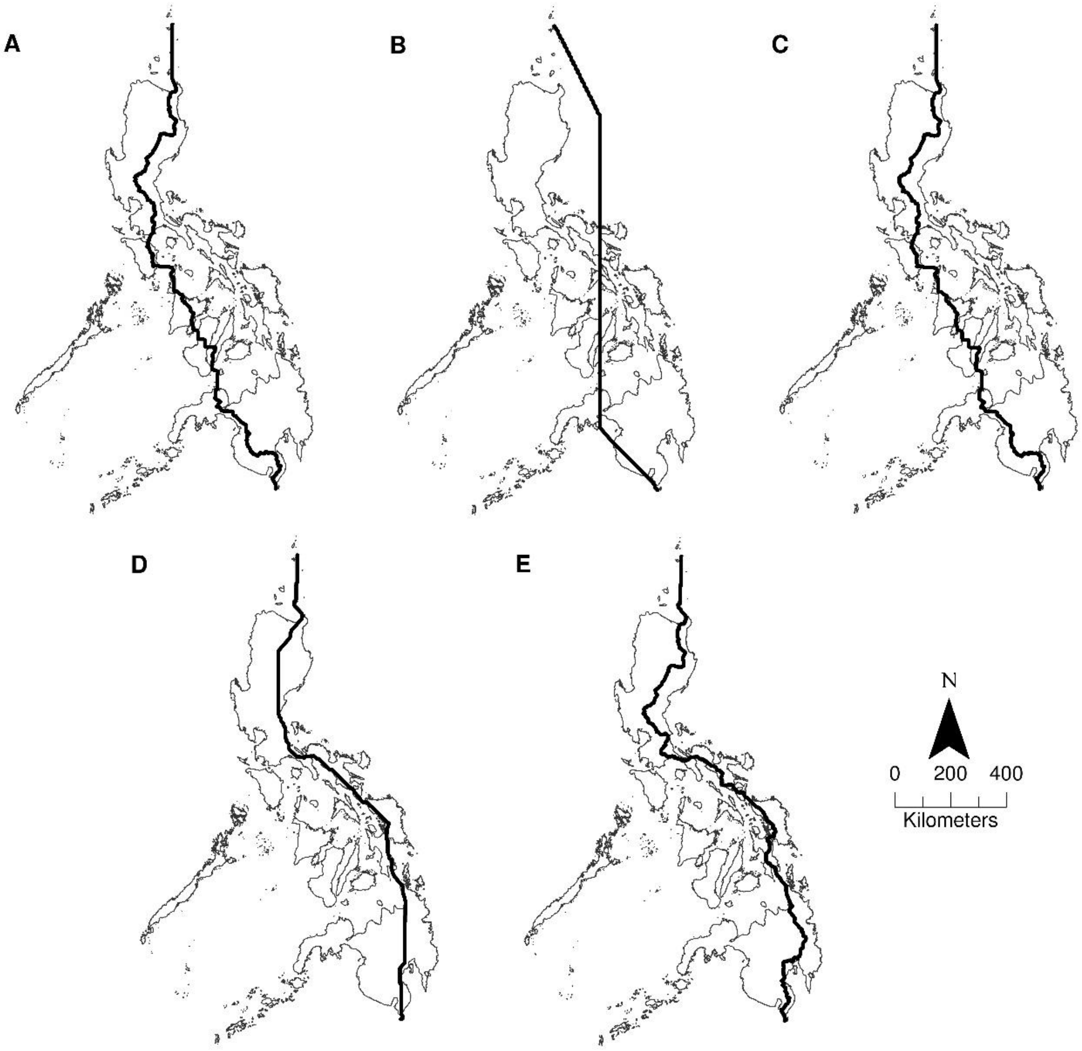

Figure 2. Migratory routes of hypothetical Grey-faced Buzzards migrating through the Philippines modeled using 5 different cost of movement datasets and exiting the country at Balut Island (because of space considerations, modeled routes to four other exit points are shown in the SI). Modeled routes demonstrate trade-offs between response to external factors and were modeled using (A) costs of moving between stopover sites only (2,408 km); (B) cost of wind direction only (1,810 km); (C) combined costs of stopover distances and wind direction (2,410 km); (D) combined costs of wind direction and over-water travel (1,981 km); and (E) combined costs of distances between stopover sites, costs of wind direction and over-water travel (2,506 km).

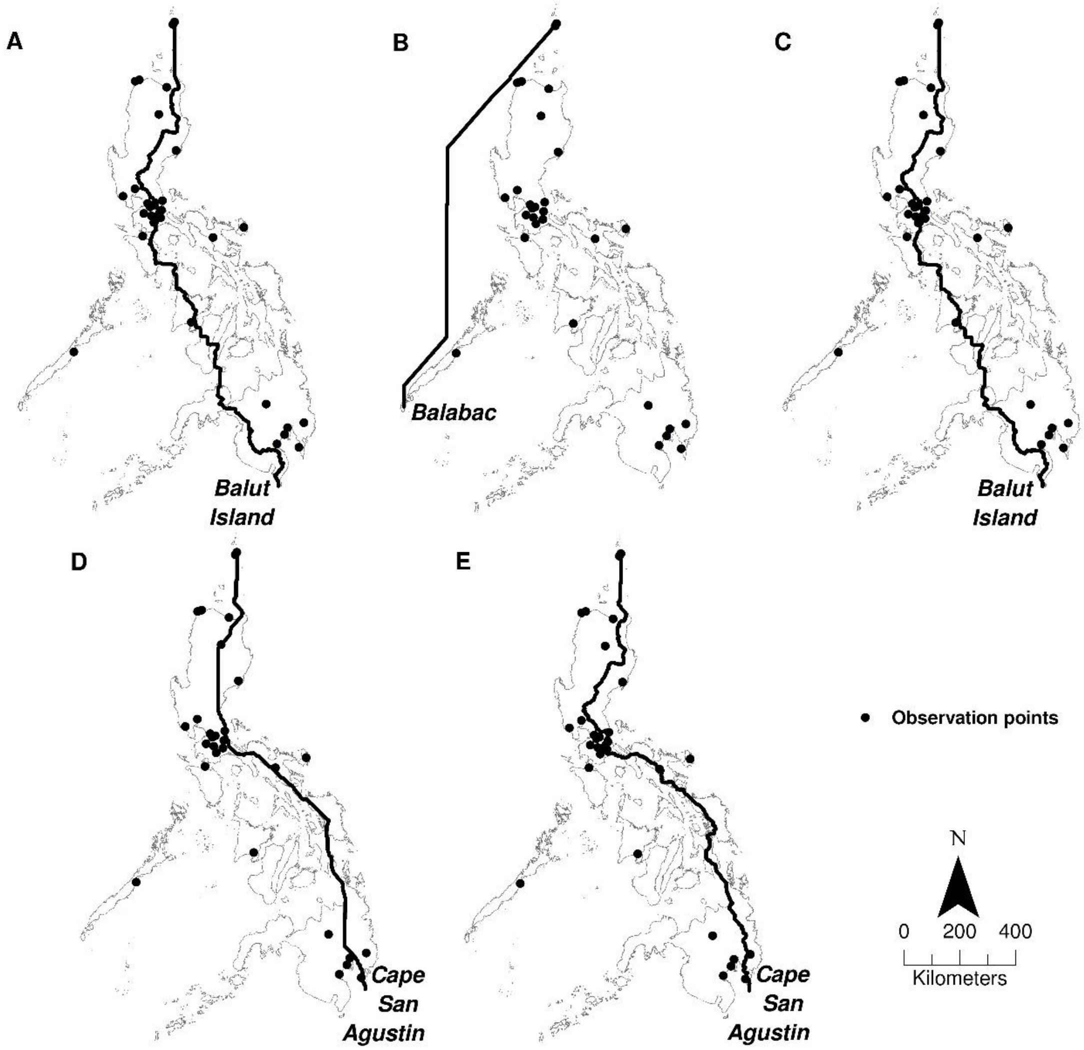

Figure 3. Least costly (in terms of movement costs) migratory route alternatives based on different migration strategies of hypothetical Grey-faced Buzzards. Migration strategies considered (A) stopover distances only; (B) wind costs only; (C) stopover distances * wind costs; (D) wind costs * over-water costs; and (E) wind costs * over-water costs * stopover distances. Also shown is the distribution of observation points (⍰) of Grey-faced Buzzards during migration. Observation points (n=29) were compiled from published, citizen-science and personal data and illustrate how modeled routes correspond to observed buzzard behavior.

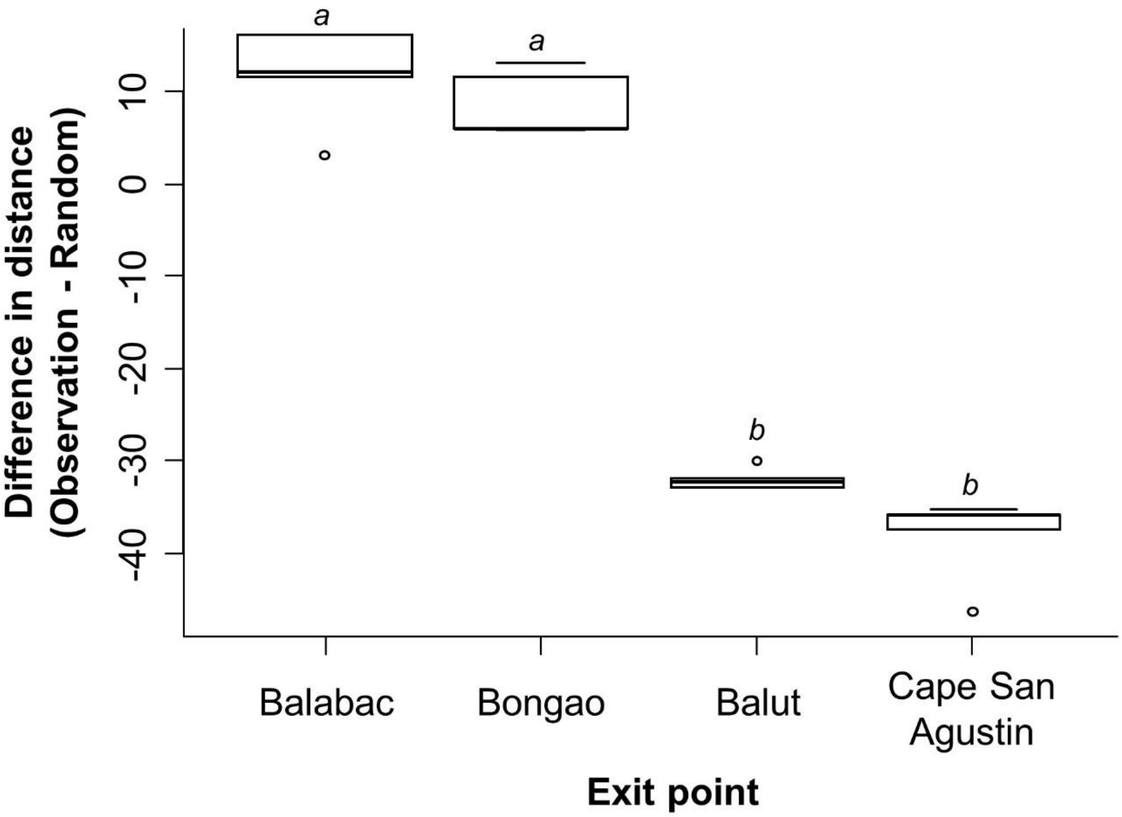

Figure 4. Difference in distances of observations of Grey-faced Buzzards and random points to modeled routes grouped according to exit point. There are 5 modeled routes for each exit point. When observation points are closer on average to the routes, the difference is positive. When observation points are farther on average to the routes, the difference is negative.

Table A1. Land cover classifications according to the Global Land Cover (GLC) 2000 dataset (GLC 2003).

Cell value	Description
0	Sea
1	Tree cover, broadleaved, evergreen, closed and closed to open
2	Mosaic: Tree cover / Other natural vegetation or cropland (including very degraded and open tree cover)
3	Tree cover, broadleaved, deciduous, mainly open (including dry Dipterocarpus)
4	Tree cover, regularly flooded; Mangrove
5	Tree cover, regularly flooded; Swamp
6	Mosaics and shrub cover, shrub component dominant, mainly evergreen
7	Mosaics and shrub cover, shrub component dominant, mainly deciduous
8	Shrub cover, mainly deciduous (Dry or burnt)
9	Mosaic of cropland / Other natural vegetation (Shifting cultivation in mountains)
10	Herbaceous cover (including alpine grassland)
12	Cultivated and managed, non-irrigated (mixed)
13	Cultivated and managed, irrigated (flooded, rice, shrimp farms)
15	Snow and ice
16	Artificial surfaces
17	Water bodies
18	No data

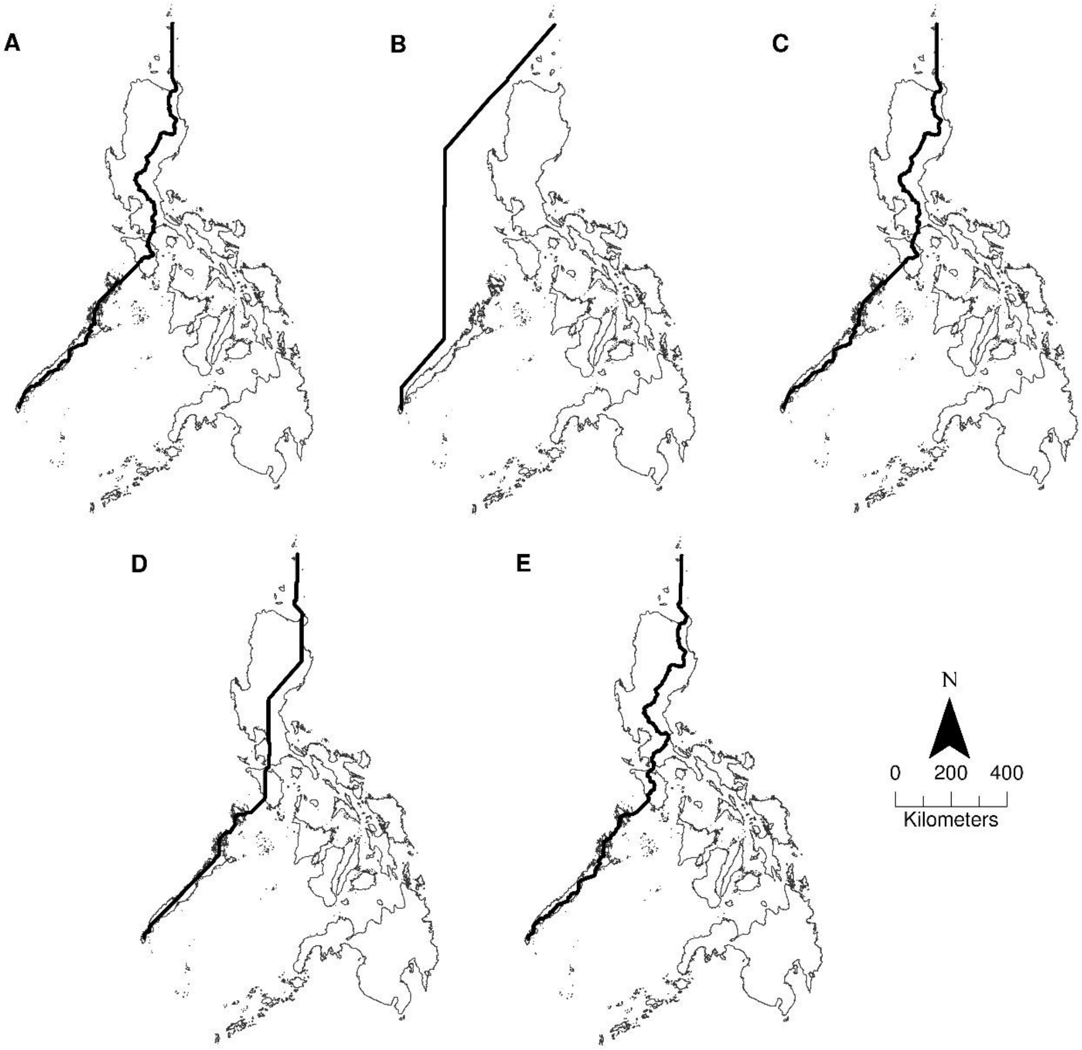

Figure A1. The five migratory routes of hypothetical Grey-faced Buzzards exiting through Balabac modeled using (A) costs of moving between stopover sites only (1,923 km); (B) cost of wind direction only (1,582 km); (C) combined costs of stopover distances and wind direction (1,923 km); (D) combined costs of wind direction and over-water travel (1,662 km); and (E) combined costs of distances between stopover sites, costs of wind direction and over-water travel (2,011 km).

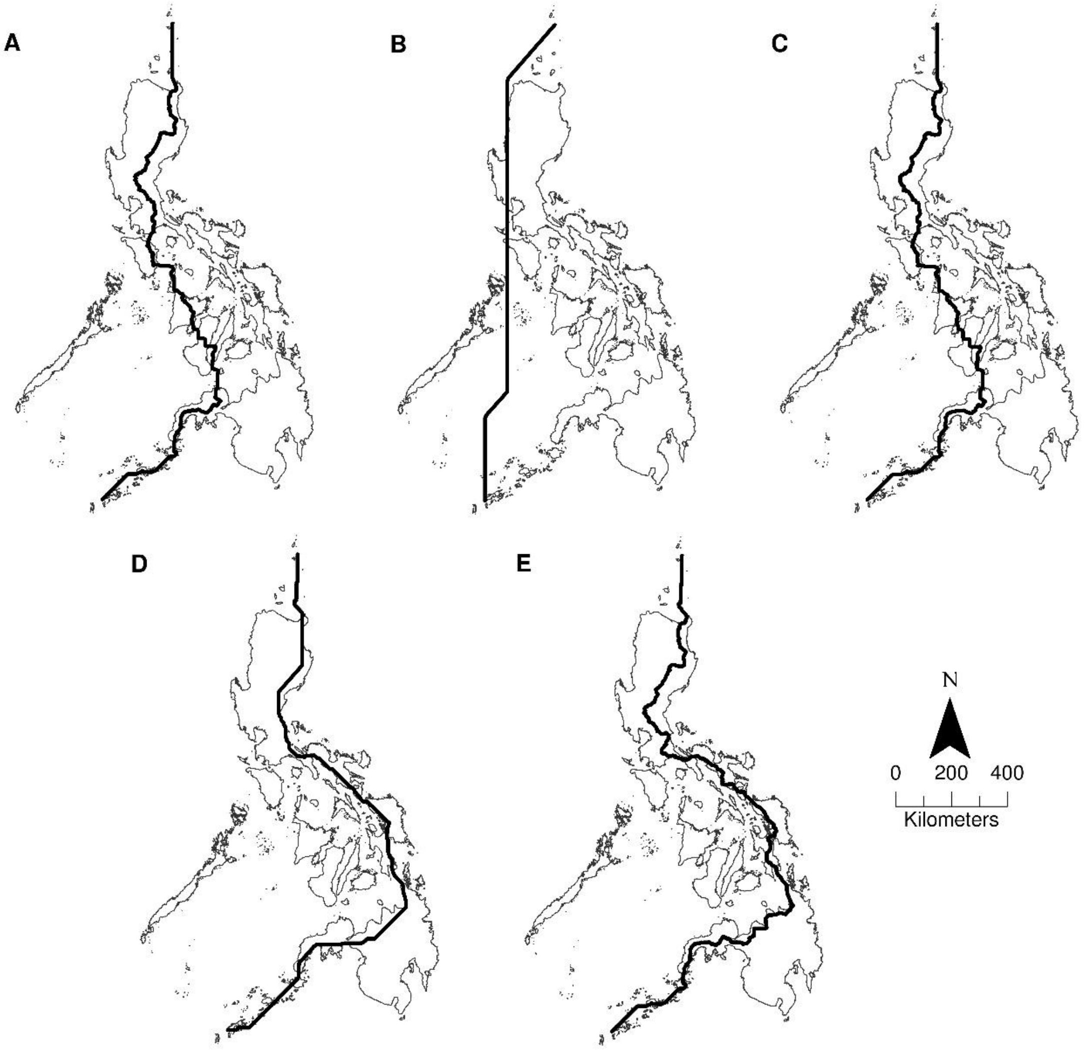

Figure A2. The five migratory routes of hypothetical Grey-faced Buzzards exiting through Bongao modeled using (A) costs of moving between stopover sites only (2,527 km); (B) cost of wind direction only (1,798 km); (C) combined costs of stopover distances and wind direction (2,517 km); (D) combined costs of wind direction and over-water travel (2,419 km); and (E) combined costs of distances between stopover sites, costs of wind direction and over-water travel (2,970 km).

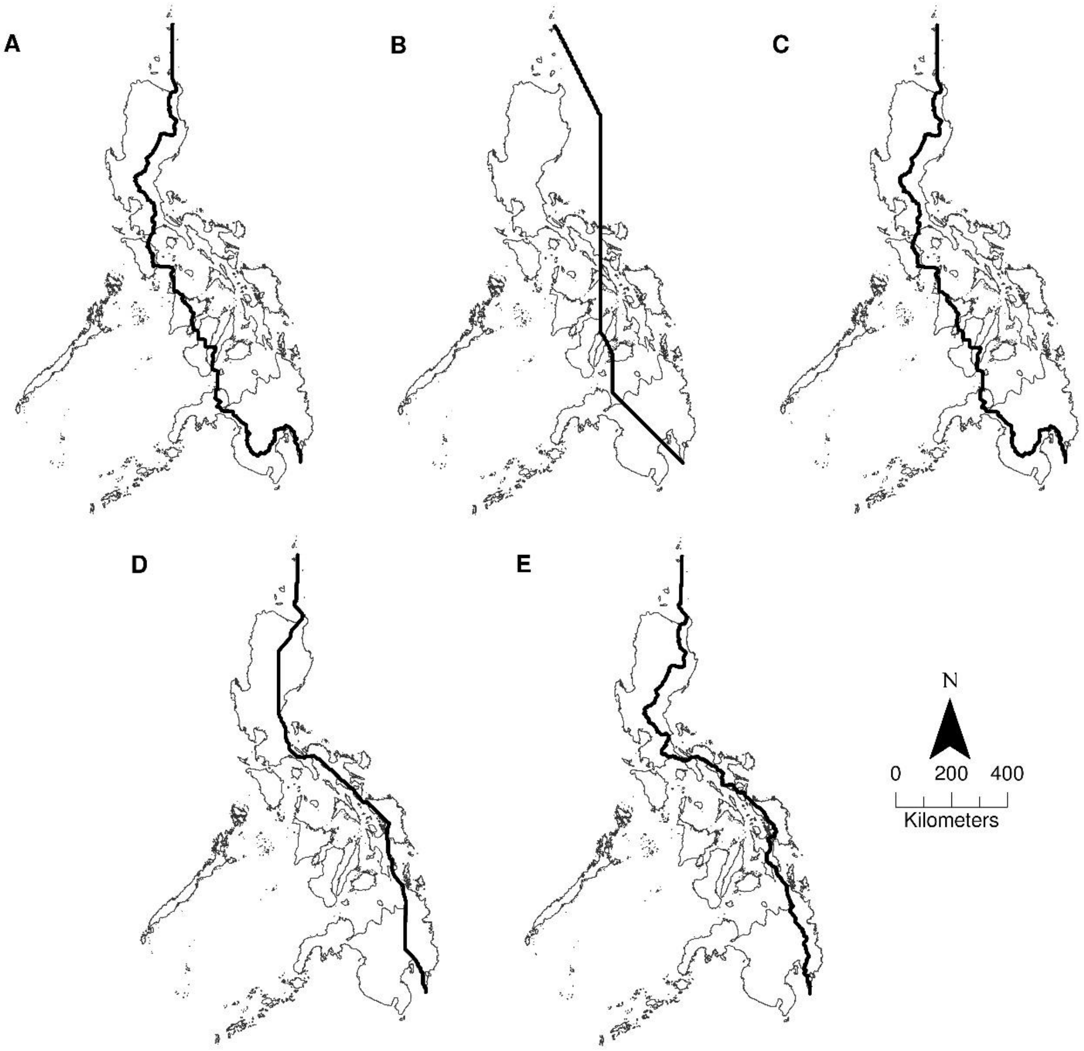

Figure A3. The five migratory routes of hypothetical Grey-faced Buzzards exiting through Cape San Agustin modeled using (A) costs of moving between stopover sites only (2,536 km); (B) cost of wind direction only (1,750 km); (C) combined costs of stopover distances and wind direction (2,535 km); (D) combined costs of wind direction and over-water travel (1,900 km); and (E) combined costs of distances between stopover sites, costs of wind direction and over-water travel (2,355 km).