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Author: Concepcion, Camille B.

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SPECIES COMPOSITION, TIMING, AND WEATHER CORRELATES OF AUTUMN OPEN-WATER CROSSINGS BY RAPTORS MIGRATING ALONG THE EAST-ASIAN OCEANIC FLYWAY

Camille B. Concepcion[1]
Division of Forestry and Natural Resources, West Virginia University, Morgantown WV 26506 U.S.A.

Patricia T. Dumandan
University of the Philippines Mindanao, Mintal, Davao City 8022 Philippines

Medel R. Silvosa
Davao del Norte State College, New Visayas, Panabo 8105 Philippines

Keith L. Bildstein
Hawk Mountain Sanctuary, 1700 Hawk Mountain Road, Kempton, PA 19527 U.S.A.

Todd E. Katzner
Division of Forestry and Natural Resources, West Virginia University, Morgantown WV 26506 U.S.A.
and
U.S. Geological Survey, Forest & Rangeland Ecosystem Science Center, 970 Lusk St., Boise, ID 83706 U.S.A.

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 raptors 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.*

LA COMPOSICIÓN DE ESPECIES, FENOLOGÍA Y LA METEOROLOGÍA SE CORRELACIONAN CON EL CRUCE DE MAR ABIERTO DE AVES RAPACES QUE MIGRAN A LO LARGO DE LA RUTA MIGRATORIA OCEÁNICA DEL ESTE ASIÁTICO

Resumen.—La migración de rapaces raramente implica movimientos de larga distancia a través de mares abiertos. Una excepción sucede a lo largo de la Ruta Migratoria Oceánica del Este Asiático. Obtuvimos

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[1] Email address: cbconcepcion@gmail.com

datos de migración en dos puntos terrestres de observación de rapaces a lo largo de esta ruta migratoria para comprender mejor los movimientos sobre mar abierto a lo largo de este corredor ubicado en su mayor parte sobre el agua. Durante el otoño de 2014, en el extremo norte de Filipinas, en Basco, Isla de Batan, registramos 7587 rapaces migratorias. Cerca del extremo sur de Filipinas, en el Cabo San Agustín, ubicado en la Isla de Mindanao, registramos 27,399 rapaces migrando en otoño de 2012. *Accipiter soloensis* fue la especie observada con mayor frecuencia, constituyendo aproximadamente el 89% y el 92% de los registros totales en Basco y Cabo San Agustín, respectivamente. *Butastur indicus* fue la segunda especie rapaz migratoria, constituyendo el 8% del total de los conteos en ambos lugares de observación. El periodo de migración comenzó de una a dos semanas antes en Basco, el lugar más septentrional, que en Cabo San Agustín. Los vuelos sobre el agua en Basco mostraron sus valores más altos durante la mañana y al final de la tarde, mientras que en Cabo San Agustín hubo sólo un pico, durante la mañana. En general, la tasa de paso migratorio más elevada tuvo lugar en ambos lugares en condiciones de cielo despejado cuando los vientos fueron provenientes del noroeste. Sin embargo, observamos diferencias inter-específicas en el comportamiento migratorio en ambos lugares, con mayor probabilidad de observar accipítridos con condiciones de viento de cola o con dirección hacia el este, y mayor probabilidad de observar individuos de *B. indicus* con vientos de cara. Estos resultados contribuyen a la caracterización de aspectos poco conocidos de la biología de aves rapaces y a identificar potenciales cuellos de botella migratorios o sitios clave para la conservación de rapaces en los ecosistemas tropicales poco estudiados de Filipinas.

[Traducción del equipo editorial]

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°27.08′N, 121°57.85′E). The lighthouse has a panoramic view of the northern part of Batan Island, as well as 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°16.78′N,

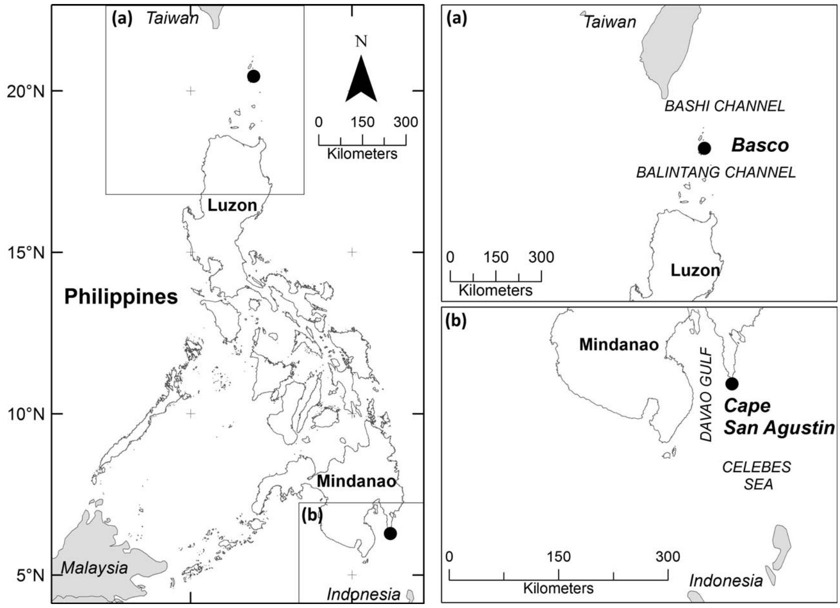

Figure 1. Geographic locations of watchsites in the Philippines where migration counts were conducted in 2012 (Cape San Agustin) and 2014 (Basco). Map on the left shows the entire Philippines with the location of watchsites (•). The top right inset (a) shows the location of the watchsite at Basco and 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 on the island of Mindanao, as well as the northernmost islands of Indonesia (Sulawesi), 170 km south.

126°11.50′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 (i.e., passage on a northern to southern axis) or unexpected (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 m aboveground) or high (i.e., more than 30 m aboveground). 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 (Nielsen-Kellerman Company, Birmingham, MI U.S.A.) and at Cape San Agustin using an Anemometer HT816 (Long Term Inc., Ningbo Shi, Zhejiang Sheng, 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 1500 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 record-

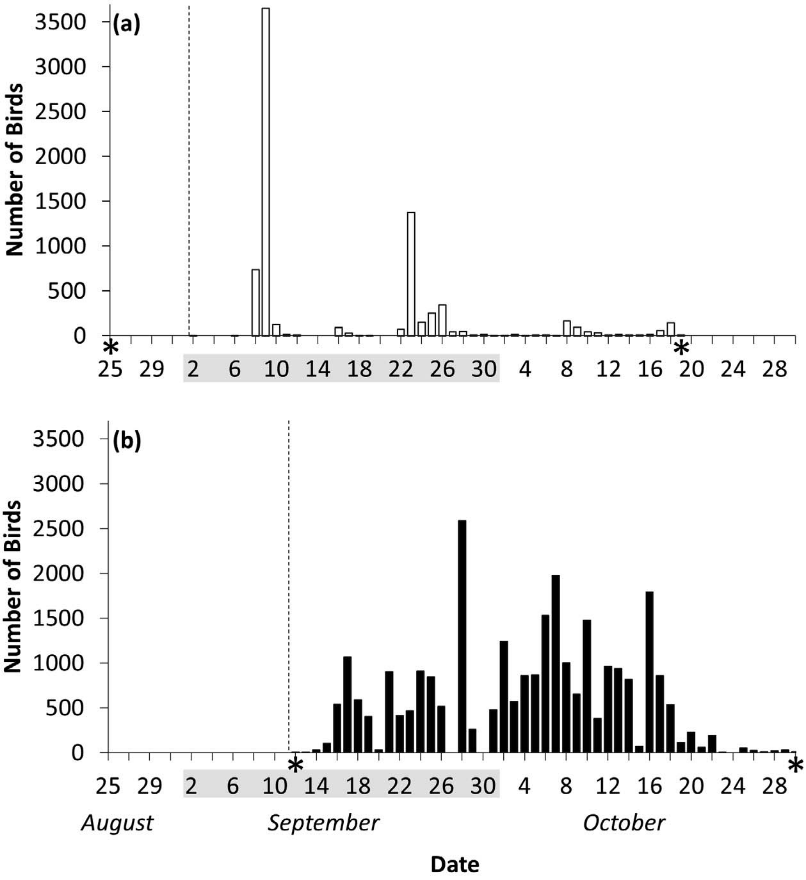

Figure 2. Within-season distribution of autumn migration flights observed at (a) Basco (25 August–19 October 2014) and (b) Cape San Agustin (12 September–30 October 2012), Philippines. Vertical dashed line shows the first day that observers were present. Asterisks show first and last days of count. These 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.

ed, 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 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 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 per 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 and Altitude 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), but 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.

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**

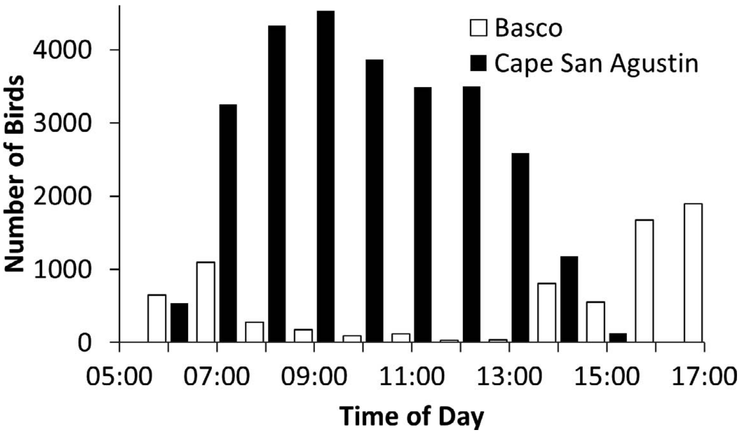

Figure 3. Time of day of autumn migration flights observed at Basco (25 August–19 October 2014) and Cape San Agustin (12 September–30 October 2012), Philippines. Migration flights were observed from 0530 H to 1730 H (Basco) and 0600 H to 1530 H (Cape San Agustin).

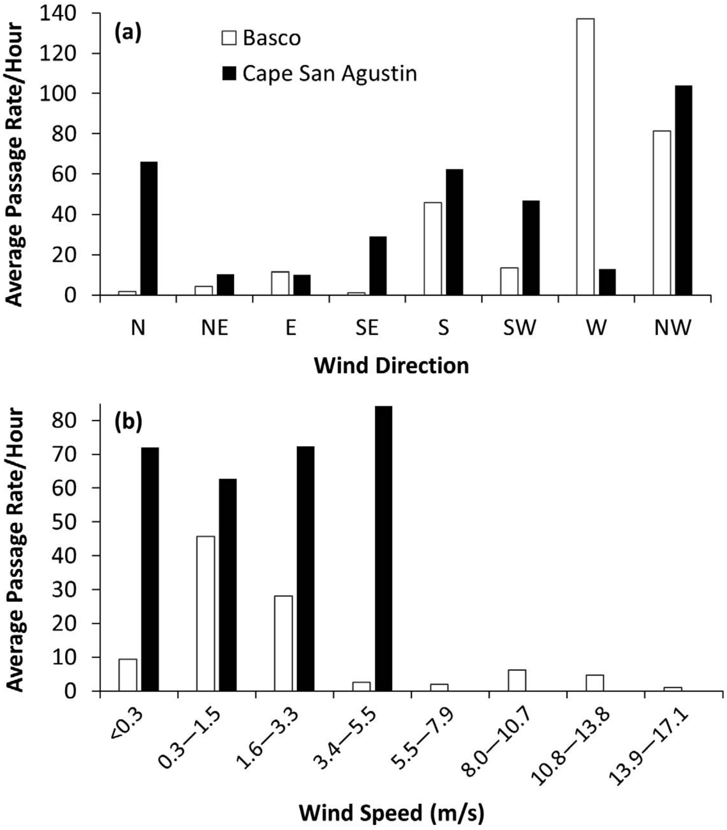

Figure 4. Average passage rates of all raptors counted per hour during different (a) wind directions and (b) wind speeds (m/sec) during autumn migration at Basco (25 August–19 October 2014) and Cape San Agustin (12 September–30 October 2012), Philippines. Standardized categories for wind speeds were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

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 ($\geq$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 midday.

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

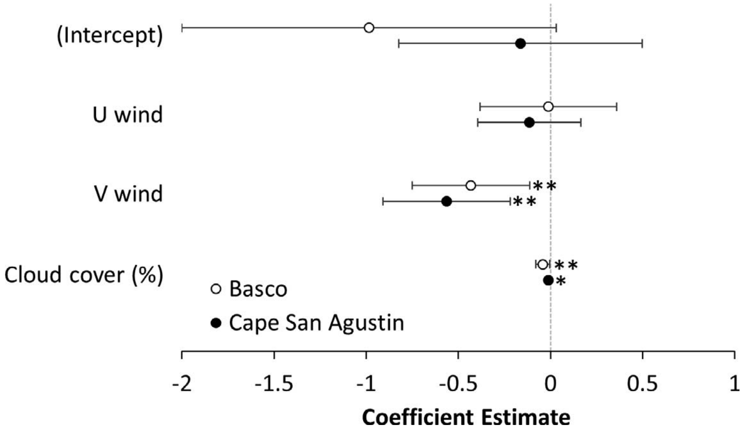

Figure 5. Coefficient estimates for generalized linear mixed models for weather conditions associated with hourly autumn passage rates for Basco (25 August–19 October 2014) and Cape San Agustin (12 September–30 October 2014), Philippines. U and V wind components were measured using handheld, digital 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 $P < 0.001$).

(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).

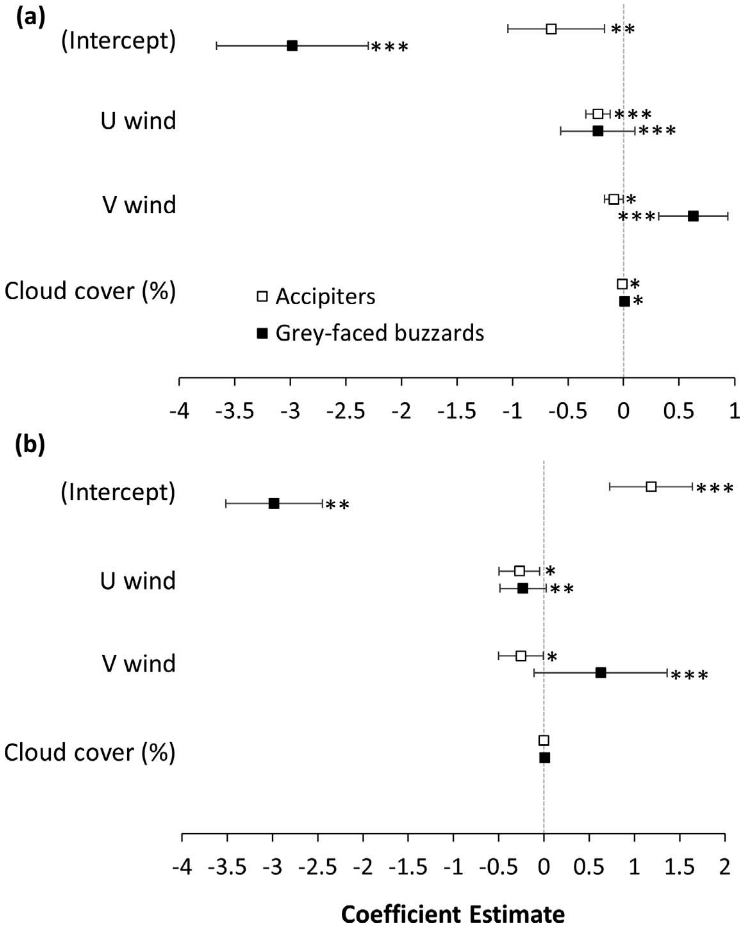

Figure 6. Coefficient estimates for generalized linear model for weather conditions associated with Accipiter and Grey-faced Buzzard hourly autumn passage rates for (a) Basco (25 August–19 October 2014) and (b) Cape San Agustin (12 September–30 October 2012), Philippines. U and V wind components were 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 $P < 0.001$).

At Cape San Agustin, the odds of observing *Accipiters* increased with tailwinds and eastward winds (Fig. 6b). In contrast, the odds of observing Grey-faced Buzzard passage increased with headwinds and westward winds (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 at 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 over water, 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 knowledgable 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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