**Selection of migratory routes by neotropical migrants along a coastal area in Costa Rica**

Kas A. Koenraads1

*Applied Biology course, University of Applied Sciences HAS Den Bosch, P.O. Box 90108,*

*‘s-Hertogenbosch, The Netherlands*

13 July 2013

**ABSTRACT.** The use of migratory routes by neotropical migrants along the immediate coastline and an inland forest area was studied on a small scale. Actively migrating birds were visually recorded along the Caribbean coast in northern Costa Rica during spring migration 2013. Counts were conducted between 07.00 and 17.00 hr on two sites: one on the immediate coastline and one in a forest area 250 m inland. Most species counted were Cliff swallow, Barn swallow, Bank swallow, Chimney swift, and Eastern kingbird. More swallows were observed along the immediate coastline, whereas Chimney swift and Eastern kingbird were recorded significantly more often along the inland forest. The results might indicate that swallows prefer flying along immediate coastlines and Chimney swifts and Eastern kingbirds might fly along inland forest areas. Swallows possibly used the coastline for favourable flying conditions and as a landmark to orient themselves for wind drift compensation. Chimney swifts are probably more efficient in compensation and might prefer foraging conditions in forested areas. Eastern kingbirds might migrate along inland forest for orientation on suitable foraging habitat.

***Key words***: bird migration, coastline, Costa Rica, inland forest, route selection, small scale

It is suggested that long-distance migratory birds benefit from their migratory strategy: a higher reproductive success by breeding in temperate, food rich areas with little competition combined with better chances of survival by wintering in temperate tropical areas (Greenberg 1980). More than two-thirds of the breeding bird species from temperate North America migrate to wintering grounds in the Caribbean, Mexico, Central and South America (Keast and Morton 1980, Rappole 1995). Migration happens over a large spatial scale, but over a relatively short temporal scale, which restricts the time and energy reserves available for migrant birds (Moore et al. 2005). Landmarks, like coastlines, can be used for wind drift compensation and are known to have a leading function for migratory birds (Åkesson 1993, Alerstam and Pettersson 1977, Berthold 2000, Richardson 1991). Wind can be an influential factor in timing, navigation, and energy costs as migratory birds spend a long time in the air and cover long distances. As they cannot hide from wind during their flight they take the risk of being geographically displaced as a result of wind drifts. Several studies suggest that migratory birds increase efficiency of energy and time use during their flight by compensating for these drifts (Alerstam 1979, Liechti 1995). Coastlines can be used for orientation in this compensation and flight direction (Åkesson 1993, Alerstam 1990, Bingman et al. 1982).

Corresponding author. Current address: Oude

Hushoverweg 60, 6003 AN, Weert, The Netherlands

Email: kas.koenraads@xs4all.nl

2 The habitat where a migratory bird pauses between migratory flights

**Coastal migration.** Alerstam (1990) states that diurnal migrants might have benefits of using coastlines during migration in three  
  
  
main ways: 1) geographical landmarks can be used for orientation; 2) in wind conditions with high risks for wind drift birds can save time and energy by migrating along coastlines (Alerstam and Pettersson 1977); and 3) reducing mortality risks by avoiding crossings of ecological barriers, for example to reduce disorientation over the sea or predation risks. This would over-compensate the extra energy demands for longer flight distances along coasts (Alerstam 1978). Coastlines probably form obvious visible and audible leading lines, even at night and for migrants at high altitudes (D'Arms and Griffin 1972, Griffin and Hopkins 1974). Some migrants seem to follow the direct coast, whereas others use a route parallel to the coastline (Richardson 1978).   
 Although selecting flying routes along coastlines can have benefits, migrants might have reasons to select other migratory routes. For example, selecting suitable stopover habitat from the air could be a reason to fly along inland areas. Eastern kingbirds *Tyrannus tyrannus* for example, seem to select open habitats and might focus on fruit trees, one of their food sources, during migration (Morton 1971, Moore and Woodrey 1993). Aerial feeders, like swallows and swifts, are considered to refuel while flying as they are not forced to use stopover sites, like many other migrants do (Davis 1965, Ormerod 1991). Thus, aspects like foraging behaviour and selection of stopover habitat might have influence on selection migratory routes as well.

**Orientation and drift compensation.** It has been predicted that migrating birds could reduce energy costs and time during their flight when using strategies to compensate for wind drifts. Their adaptive drifts depend on the wind direction and strength and on the distance to their destination (Alerstam 1979, Liechti 1995). Migrants may selectively fly on higher altitudes when the preferred direction is downwind, as winds generally get stronger with increasing altitude. Drift, partial compensation and full compensation can occur; with increasing wind speed and increasing altitude the degree of compen-sation decreases (Bruderer and Jenni 1988, 1990, Bruderer & Liechti 1990). When the preferred heading is different from the wind direction, however, migrants may stay on the ground or fly at lower altitudes, where wind speeds are generally lower and compensating for drifts is easier (Bingman et al. 1982). Several studies have investigated in which manner migrating birds compensate for these wind drifts (Alerstam 1976, Richardson 1991, Liechti 2006). These studies show that birds use complex orientation responses, which are very variable and can differ from partial to full and even overcompensation. Although the use and variability of different techniques is poorly understood, it is suggested that the behaviour in this compensation can differ between species, flight conditions and ages. Age differences could be noticeable between spring and fall migration, as young and inexperienced birds make up part of the migrants during fall migration (Berthold 2001). Moreover, juvenile birds may be less able to compensate for drifts (Berthold 2001) and, as they lack experience, use less complex navigation systems that don’t allow them to correct for geographical displacements like experienced birds do (Åkesson 2003, Thorup et al. 2003, 2007). However, basic reoriented migration as a response to flying along coastal areas might be inborn (Alerstam, 1978).

Selection of migratory routes along coastlines or inland areas is expected to depend mainly on the species, flying conditions, foraging behaviour and use of stopover sites (Alerstam and Pettersson 1977, Bingman et al. 1982, Karlsson et al. 2010, Moore and Woodrey 1993, Morton 1971, Richardson 1978, 1991, Waugh & Hails 1983, Winkler 2006). It is hypothesised here that these aspects mainly determine if migrants follow coastlines or inland areas and coastlines are used more because of favourable flying conditions, depending on the species. The strategies used by spring migrants to determine which part of coastal areas they select as stopover habitat[[1]](#footnote-1) has been studied on a large scale in Mississippi (Moore et al. 2005). They observed more migrant birds stopping over in inland forest areas far away from the coast than close to the coastline. However, how flying routes along coastal areas are selected by neotropical migrants has not been studied yet, especially not on a small scale. In this study it was investigated whether long-distance migratory birds use immediate coastlines or inland forest areas as migratory routes on a small scale. Diurnal migration counts were conducted to monitor spring migration in a Caribbean coastal area in northern Costa Rica and to make a comparison between usage of both routes. Habitat use and time spent in stopover sites was not studied, but would be a meaningful addition in under-standing selection of migratory routes by migrant birds.

**METHODS**

**Study area.** During the period 1 March 2013 until 24 May 2013 migration counts were conducted in two areas located on the northeast coast of Costa Rica within 7 km of the village of Tortuguero, Limón Province (Latitude 10°59' N; Longitude 83°52' W). The monitoring areas are situated in the 19,211-ha Tortuguero National Park and the adjacent Barra del Colorado National Wild-life Refuge (Ralph et al. 2005). This lowland region is dominated by the Holdridge (1987) forest type, which is described as Very Wet Broadleaf Tropical Forest. The area counts several rivers and canals and is increasingly changed for mainly agricultural use. The average annual temperature in the region is 29.9° C and the mean annual precipitation is >5000 mm, which makes it the wettest region of Costa Rica.

In both areas migration counts were conducted from a fixed point. These points were located within 1 km of the Caribbean Sea and provided an open view on migrants flying over. The fixed point of location 1 (Latitude 10°35’36’’ N; Longitude 83°31’39’’ W) is situated on the Caño Palma Biological Station property. The point is located on the border of secondary rainforest and the station’s garden, approximately 250 m inland. The Caño Palma river borders this area on the East side. On location 2 a fixed point (Latitude 10°35’44’’ N; Longitude 83°31’31’’ W) located 20 m off the coastline on a sand beach, separated from agricultural lands by palm trees, was used. The two locations are separated by the Caño Palma River and a large hotel garden. See fig. 1 for a global map and a detailed map of the area with locations of the fixed points.

**Migration counts.** The standardized method described by Ralph et al. (1993, 2005) and recommended by the Partners In Flight (Aves de las Américas) Monitoring Working Group (Hussell and Ralph 1998), was used to conduct diurnal migration counts. 91 counts were done in each monitoring area, on respectively 17 and 18 different days on location 1 and 2. The counts were conducted within 30-min periods centered on 07:00, 09:00, 11:00, 13:00, 15:00, and 17:00 hr (for example, start time of the first count was between 06.45 and 07.15). The counts were 10-min scans of the sky facing south, as they were focused on migrants heading north, back to their breeding grounds in North-America. A minimum of five counts a day was needed following the standardized method. Thus, counts were normally conducted 50-60 min a day, depending on weather conditions and schedule. During heavy showers counts were not conducted, as birds will probably not migrate in this condition. Binoculars (8×45) were only used to check identification of species if not visible with the naked eye. To respect consistency of the method additional birds during the check with binoculars were not recorded as they were not observed with the naked eye first. During the counts only the actively migrating birds which flew overhead in a straight direction were recorded using a protocol (App. I). Swallows and swifts feeding during migration have been counted even when not flying in a straight direction, as the migratory species are not resident to Costa Rica and only casual or uncommon winter residents in specific regions (Stiles and Skutch 1989). Temperature, cloud cover (%), precipitation, and wind speed and direction were also recorded following the standards noted in the protocol.

|  |
| --- |
| C:\Users\Kas\Desktop\Knipsel.JPG  **Fig. 1.** Area map with the locations (red stars) from which migration counts were conducted on the im-  mediate coastline (1) and inland forest area (2) on the coast of the Caribbean sea in Tortuguero area. |

**Data analysis.** The most numerous migratory species were used in this analysis. To determine which species were most numerous the amount of individuals counted per species was compared to the total amount of all individuals counted. The Shapiro-Wilk test was used to determine   
 normality of data (max. P-value < 0,01, max. W-value(182) = 0,306). Levene’s test was used to determine homogeneity of variances, which showed significant and insignificant results for different species (max. P-value < 0,01 and max. F-value(180) = 44,678 for Chimney swift and Eastern kingbird; min. P-value = 0,592 with F-value(180) = 0,288 for Barn swallow, Cliff swallow, and Bank swallow). No transformation was beneficial. As none of the species’ data showed a normal distribution a binary analysis was used instead. A Generalized Estimating Equations (GEE) analysis based on binary logistic data was performed. All analyses were performed using SPSS 17.0 software.

**RESULTS**

During the entire study 6126 birds were counted, of which 665 along the inland forest (location 1) and 5461 along the immediate coastline (location 2). A number of 17 species could be identified, of which the five most numerous ones, in order of abundancy, were Cliff swallow *Petrochelidon pyrrhonota*, Barn swallow *Hirundo rustica*, Bank swallow *Riparia riparia,* Eastern kingbird *Tyrannus tyrannus*, and Chimney   
swift *Chaetura pelagica*. These species represent 5960 of the total 6126 individuals counted. See table 1 for exact numbers of the five species. Of all individuals counted one individual swift could not be identified. The five species account for respectively 95,6% and 97,5% of all individuals counted on location 1 and 2. The total number of occasions on which these species were encountered during counts are shown in table 2 for both locations 1 and 2.

Of all numerous migrants counted, the share in flying along the immediate coastline (2) was 89,3%, whereas this was 10,7% for migrants flying along the inland forest area (1). Among the species using the immediate coastline were primarily swallows: Cliff swallow, Barn swallow, and Bank swallow. Along inland forest areas the dominant species counted were Eastern Kingbird and Chimney swift.

A difference was found for the number of occasions on which Barn swallow (Wald

Chi-square = 5,922E29; P < 0,01), Bank swallow (Wald Chi-square = 5,843; P = 0,016), and Chimney swift (Wald Chi-square = 2,261E31; P < 0,01) were observed on location 1 and location 2. For American cliff swallow no difference was found between the amount of occasions counted on location 1 and 2 (Wald Chi-square = 0,000; P = 0,985). Eastern kingbird was counted during 3 of 91 counts (total of 196 individuals) on location 1 and during 0 of 91 counts on location 2. For this species no analysis could be performed with SPSS as a result of lacking positive values on location 2, which impeded the model from running the analysis.

The chance of counting Barn swallow (0,146 > 0; P < 0,01) and Bank swallow (1,317E-16 > 0; P = 0,016) was higher on location 2 than on location 1. American cliff swallow (-5,902x 10^-18 < 0; P = 0,985) and Chimney swift (-2,004 < 0; P < 0,01) showed a higher chance of being counted on location 1 than on 2. A summary of the GEE analysis results for all five species is given in table 2.

**Table 1.** Absolute amounts and portions of the five most numerous migratory species counted on monitoring locations (1 = inland forest, 2 = immediate coastline) .

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Species**  **Location** | *Petrochelidon pyrrhonota* | *Hirundo rustica* | *Riparia*  *Riparia* | *Tyrannus tyrannus* | *Chaetura*  *pelagica* | ***Total*** |
| **1** | 227  (35,70%) | 122  (19,20%) | 11  (1,70%) | 196  (30,80%) | 80  (12,60%) | 665 (100%) |
| **2** | 3482  (65,40%) | 1625  (30,52%) | 204  (3,83%) | 0  (0,00%) | 13  (0,24%) | 5324  (100%) |

**Table 2.** Total number of occasions on which species were encountered on each location (1 = inland forest, 2 = immediate coastline) and results of analysis (GEE, binary logistic).

|  |  |  |  |
| --- | --- | --- | --- |
| **Species** | **# encounters on 1** | **# encounters on 2** | **chance of encountera** |
| *Petrochelidon pyrrhonota* | 3 | 3 | -5,902 x 10^-18; P = 0,985 |
| *Hirundo rustica* | 7 | 8 | 0,146; **P < 0,01** |
| *Riparia riparia* | 1 | 1 | 1,317 x 10^-16; **P = 0,016** |
| *Tyrannus tyrannus* | 3 | 0 | - - |
| *Chaetura pelagic* | 13 | 2 | -2.004; **P < 0,01** |
| a Positive value = higher encounter chance on 2; negative value = higher encounter chance on 1. Significant difference between number of encounters on locations in bold (when P < 0,05). | | | |

**DISCUSSION**

All swallow species were observed in higher amounts along the immediate coastline, whereas higher numbers of Chimney swifts and Eastern kingbirds were counted along the inland forest area. No difference was found between the amount of occasions on which Cliff swallow and Bank swallow were observed on both locations. Barn swallows were counted on the immediate coastline on more occasions than in the inland forest area. Chimney swifts and Eastern kingbird were observed along the inland forest location during more occasions. Absolute amounts of migrating birds give a better indication of the use of the two migrational routes, but these could not be analyzed as they contained too many 0 values. A binary analysis was used instead, in which differences between the number of occasions on which a species was encoun-tered were analyzed. The higher amounts of swallows counted along the immediate coastline are possibly related to favourable flying and foraging conditions and the ability to compensate and orient for wind drifts. Cliff swallow and Bank swallow were much more numerous on the immediate coastline than in the inland forest area, although a difference in encounter chance was only found for Bank swallow. As it concerned only one observation for both locations no difference was expected. For Barn swallow and Chimney swift the expected result was found, which supports the higher absolute number of Barn swallow along the coastline and higher amount of Chimney swifts along the inland forest. The difference between route selection of swallows and swifts might be related to the more efficient compensation abilities and foraging preference above forest areas of swifts. The binary analysis could not be used for Eastern kingbird, as the species was not counted on the immediate coastline. Eastern kingbirds were observed on the inland forest area during multiple counts. Worth mentioning is though, that Eastern kingbirds were never found present on the ground near the inland forest, but were seen in trees close to the immediate coastline on several occasions. These observations suggest that the species actively migrated along the inland area, but spent time on the ground in the areas closer to the coastline. Different use of both locations could be related to feeding on fruits and insects in more open habitat and flying along forest areas with views on fruiting trees.

**Drift compensation and landmark use.** The wind recorded during this study was generally strong and mainly heading west - on some occasions northwest. This coastal side wind drift could have an influence on the direction of migrants heading northwards. All five migrant species were recorded flying over at relatively low altitudes (estimated at max. 400 m, but in most cases within 100 m), although Chimney swift generally flew higher than swallows and kingbirds. Several studies show that wind conditions can be more favourable at low altitudes and landmarks can be used for orientation in wind drifts during migration. For example, a study of Bingman et al. (1982) near the Hudson river in New York area showed that under specific circumstances (close to a river and with low flight altitudes) nocturnal fall migrants seemed to follow landmarks, like a river, when the wind direction was different from the preferred direction. By doing this they showed a drift compensation to orient themselves instead of being drifted by the wind. In favourable wind conditions they did not seem to fly parallel to the river, which implies that migrants heading southwest did not always use the river as a landmark to orient on. Results from a study on nocturnal passerine migrants, flying on low altitudes along two adjacent coastal areas in southwestern Sweden showed that migrants flew along coastlines and in some cases used the coastline to compensate partially or completely for wind drifts (Åkesson 1993). The studies mentioned focused on nocturnal migrants, but the use of coastlines and drift compensation to fly in preferred direction are also found in diurnal migrants (Alerstam and Pettersson 1977, Richardson 1991).

Both factors, flight altitude and use of landmarks for orientation, can be recognized in the circumstances of this study. This could explain the high amounts of swallows migrating along the immediate coastline compared to the amounts flying along the inland forest area. Also the low altitude on which they generally flew over could be clarified by the suggestion that wind conditions are better on a lower altitude. Another factor for selecting routes could be orientation on suitable roosting sites, as roosting behaviour can differ among species (Winkler 2006) and roosts can be located close to the coastline (Komar 1997).

**Foraging behaviour.** Another reason for flying low could be the food abundance in the air. According to Johnson (1957) the aerial insect abundance decreases with altitude. Flying on lower altitudes might therefore be advantageous for birds that generally feed on the wing such as swallows and swifts, however might also provide benefits for Eastern kingbirds, which occasionally show the same foraging behaviour (Pilastro and Magnani 1997, Baird et al. 1965, Henningsson et al. 2009).

As Chimney swift and Eastern kingbird were hardly, if at all, seen migrating along the coastline it is expected that they did not use the coastline as a landmark. Other factors, like foraging behaviour and use of the area as stopover site, could influence the route they follow as well. Chimney swifts might prefer forest as foraging habitat and therefore migrate more along the inland forest area. During a study in Malaysia (Waugh & Hails 1983) several migratory and resident swift species were observed foraging over forest more than over open, agricultural habitat. Some resident breeding species like House swift *Apus nipalensis* and White-bellied swiftlet *Collocalia esculenta* preferred to feed over forest, although they built their nests on man-made structures, which were more abundant in open habitat. On the other hand, they observed Barn swallows foraging in the open area more frequently, which could indicate a different preference from the swifts studied. Higher temperatures and similarities with their breeding habitat (Medway 1973) might have been the reasons for this preference. Furthermore, they found swallows to be foraging on generally lower altitudes than the swift species. This difference is noticed during this study as well and is suggested to be related to a different diet, flight speed, manoeuvrability adaptions (Waugh & Hails 1983) and the fact that they are adapted to a life in the air, which could make orienting in the wind more efficient (Karlsson et al. 2010).

Eastern kingbirds might prefer flying along the forest area for several reasons. For example, Morton (1971) found during his study in Panama that Eastern kingbirds migrating north fly at or near treetop level and might feed on different food resources than during the southward migration. He found that large kingbird flocks migrating northwards mainly feed on fruit of *Didymopanax morototoni* trees (Araliaceae), which can be recognized from the air by the upright growth clusters of fruits they bear. All nine specimens he collected in late April had these fruits in their stomachs, whereas none of the stomachs contained insect remains and kingbirds were rarely seen hawking after insects. The behaviour of 14 individuals (five min each) was observed on occasion between 25 March and 10 May 2013 and showed a different foraging beha-viour. During 79% of the total observation time they were observed sallying at insects from a branch, whereas 2,8% of the time foraging on fruit was observed. The collected data was not statistically analysed due to a small sample size though, but did serve to complement behavioural observations. The observations were done near both monitoring locations, during which kingbirds were only seen near the ground in open habitat close to the coastline. Kingbirds likely select open habitats during their stopovers in relation with their propensity to hawk at food items (Moore and Woodrey 1993), which is also indicated by the observations done during this study. Based on this suggestion, the habitat they migrate along differs from the habitat they select for their stopover.

**Conclusions.** In short, these results indicate how several neotropical migrant species select spring migration routes on a small scale in coastal areas. It generally depended on the species and flying conditions which route was used. Swallow species generally flew on relatively low altitudes, possibly related to greater food abundance. They probably used the coastline for favourable wind conditions and as a landmark to orient on for wind drift compensation. Swifts and kingbirds migrated along inland forest areas. Swifts seemed to fly higher and probably preferred the foraging conditions above forest areas. Eastern kingbirds also flew along forest areas and probably used different areas for foraging than to migrate along.

In this study only diurnal spring migra-tion was monitored. Studying fall and nocturnal migration would be a welcome addition to the understanding of routes used by neotropical migrants. Conducting counts more actively, for example daily, might give a better image of the numbers of migrants on both locations. Further investigations on other locations and for longer time periods are required to confirm the difference among neotropical migrants in selecting their migration route on a small scale. Measuring flight altitude would also contribute to the understanding of migration and foraging behaviour of neo-tropical migrants. Additional studies on migrants’ foraging and roosting behaviour in their stopover habitat could also contribute to a better understanding of selecting migration routes.

**ACKNOWLEDGEMENTS**

This study has been made possible thanks to the Canadian Organization for Tropical Education and Rainforest Conservation and Caño Palma Biological Station, which allowed me to do observations on their property. Many thanks to Tamara Lohman, Nadja Christen, Aidan Hulatt, and Charlotte Foale for valuable comments on the paper. I am most grateful to Matt Band and Juan Rauboud for help with the GIS map and to Osama Almalik for help with the statistical analysis.

**LITERATURE CITED**

Åkesson, S. 1993. Coastal migration and wind drift compensation in nocturnal passerine migrants. Ornis scandinavica 24:87-94.

Åkesson, S. 2003. Avian long-distance navigation: experiments with migratory birds. In: Avian Migration (P. Berthold, E. Gwinner, and E. Sonnenschein, eds.), pp. 471-492. Berlin, Springer- Verlag.

Alerstam, T. 1976. Nocturnal migration of thrushes (Turdus spp.) in southern Sweden. Oikos 27:457- 475.

Alerstam, T., and S.G. Pettersson. 1977. Why do migrating birds fly along coastlines? Journal of Theoretical Biology 65:699-712.

Alerstam, T. 1978. Analysis and a theory of visible bird migration. Oikos 30:273-308.

Alerstam, A. 1979. Wind as selective agent in bird migration. Ornis Scandinavica 10:76-93.

Alerstam, T. 1990. Ecological causes and consequences of bird orientation. Experientia 46:405-415.

D'Arms, E., and D.R. Griffin. 1972. Balloonists' report sounds audible to migrating birds. Auk 89:269- 279.  
Baird, J., A. J. Meyerriecks, and A. J. Meyerreicks. 1965. Birds feeding on an ant mating swarm. The Wilson Bulletin 77(1):89-91.

Berthold, P. 2000. Vogelzug – Eine aktuelle Gesamt- übersicht. Wissenschaftliche Buchgesellschaft, Darmstadt.

Berthold, P. 2001. Bird Migration: a General Survey, 2nd edition. Oxford, Oxford University Press.

Bingman, V.P., K.P. Able, and P. Kerlinger. 1982. Wind drift, compensation, and the use of landmarks by nocturnal bird migrants. Animal Behaviour 30:49- 53.

Bruderer, B., and L. Jenni. 1988. Strategies of bird migration in the area of the Alps. Proceedings of the International Ornithological Congress 19:2150-2161.

Bruderer, B., and L. Jenni. 1990. Migration across the Alps. In: Bird Migration: Physiology and Ecophysiology (E. Gwinner, ed.), pp. 60-77. Berlin, Heidelberg, Springer-Verlag.

Bruderer B., and F. Liechti. 1990. Richtungsverhalten nachtziehender Vogel in Süddeutschland und der Schweiz unter besonderer Berücksichtigung des Windeinflusses. Der Ornitologische Beobachter 87:271-293.

Davis, P. 1965. Recoveries of Swallows ringed in Britain and Ireland. Bird Study 12:151–169.

Greenberg, R. 1980. Demographic aspects of long- distance migration. In: Migrants in the neotropics (A. Keast and E. Morton, eds.), pp. 493-516. Washington, DC , Smithsonian Institution Press.

Griffin, D. R., and C.D. Hopkins. 1974. Sounds audible to migratory birds. Animal Behaviour 22:672-678.

Henningsson, P., H. Karlsson, J. Bäckman, T. Alerstam, and A. Hedenström. 2009. Flight speeds of swifts (Apus apus): seasonal differences smaller than expected. Proceedings of the Royal Society - biological sciences 276(1666):2395-401.

Holdridge, L. R. 1987. Ecología basada en zonas de vida. 3ra reimpresión. San José, Costa Rica: Editorial del Instituto Interamericano de Cooperación para la Agricultura (IICA):216.

Hussell, D. J. T., and C. J. Ralph. [online].1998. Recommended methods for monitoring bird populations by counting and capture of migrants.http://www.fs.fed.us/psw/topics/wildlif e/birdmon/pif/migmon.html. (14 March 2013).

Johnson, C.G. 1957. The distribution of insects in the air. Journal of Animal Ecology 26:479-49.

Karlsson, H., P. Henningsson, J. Bäckman, A. Hedenström, and T. Alerstam. 2010. Compensation for wind drift by migrating swifts. Animal Behaviour 80:399-404.

Keast, A., and E. S. Morton. 1980. Migrant birds in the neotropics: Ecology, behavior, distribution, and conservation. Washington, DC , Smithsonian Institution Press.

Komar, O. 1997. Communal roosting behaviour of the Cave swallow in el Salvador. The Wilson Bulletin 109(2):332-337.

Liechti, F. 1995. Modelling optimal heading and airspeed of migrating birds in relation to energy expenditure and wind influence. Journal of Avian Biology 26:330-336.

Liechti, F. 2006. Birds: blowin’ by the wind? Journal für Ornithology 147:202-211.

Medway, L. 1973. A ringing study of migratory barn swallows in West Malaysia. Ibis 115:60-85.

Moore, F.R., and M.S. Woodrey. 1993. Stop-over habitat and its importance in the conservation of landbird migrants. Proceedings of the annual conference, Southeastern Association of Fish and Wildlife Agencies 47:447-459.

Moore, F.R., M. S. Woodrey, J.J. Buler, S. Woltmann, and T.R. Simons. 2005. Understanding the Stopover of Migratory Birds: A Scale Dependent Approach. USDA Forest Service Gen. Tech. Rep. PSW- GTR- 191. 2005:684-689.

Morton, E.S. 1971. Food and migration habits of the Eastern Kingbird in Panama. Auk 88(4):925-926.

Ormerod, S. J. 1991. Pre-migratory and migratory movements of Swallows Hirundo rustica in Britain and Ireland. Bird Study 38:170–178.

Pilastro, A., and A. Magnani. 1997.Weather conditions and fat accumulation dynamics in pre-migratory roosting Barn Swallows *Hirundo rustica*.Journal of Avian Biology 28(4):338-344.

Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin, D.F. DeSante. 1993. Handbook of Field Methods for Monitoring Landbirds. USDA Forest Service Gen. Tech. Rep. PSW-GTR-144-www. 1993.

Ralph, C.J., M.J. Widdowson, R.I. Frey, P.A. Herrera, and B.P. O’Donnell. 2005. An overview of a landbird monitoring program at Tortuguero, on the Caribbean coast of Costa Rica. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191. 2005:831-844.

Rappole, J. H. 1995. The ecology of migrant birds: A neotropical perspective. Washington, DC: Smithsonian Institution Press.

Richardson, W.J. 1978. Reorientation of nocturnal landbird migrants over the Atlantic Ocean near Nova Scotia in autumn. Auk 95:717-732.

Richardson, W.J. 1991. Wind and orientation of migrating birds: A review. In: Orientation in birds (P. Berthold, ed.), pp. 226-249. Basel, Birkhäuser Verlag.

SPSS Inc. Released 2008. SPSS Statistics for Windows, Version 17.0. Chicago: SPSS Inc.   
Stiles, F.G., and A.F. Skutch. 1989. A guide to the birds of Costa Rica. Utica, New York, Cornell University

Press, pp. 206-207, pp. 307, pp. 343-346.

Thorup, K., T. Alerstam, M. Hake, and N. Kjellén. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. Proceedings of the Royal Society – biological sciences 270 (Supplement):S8-S11.

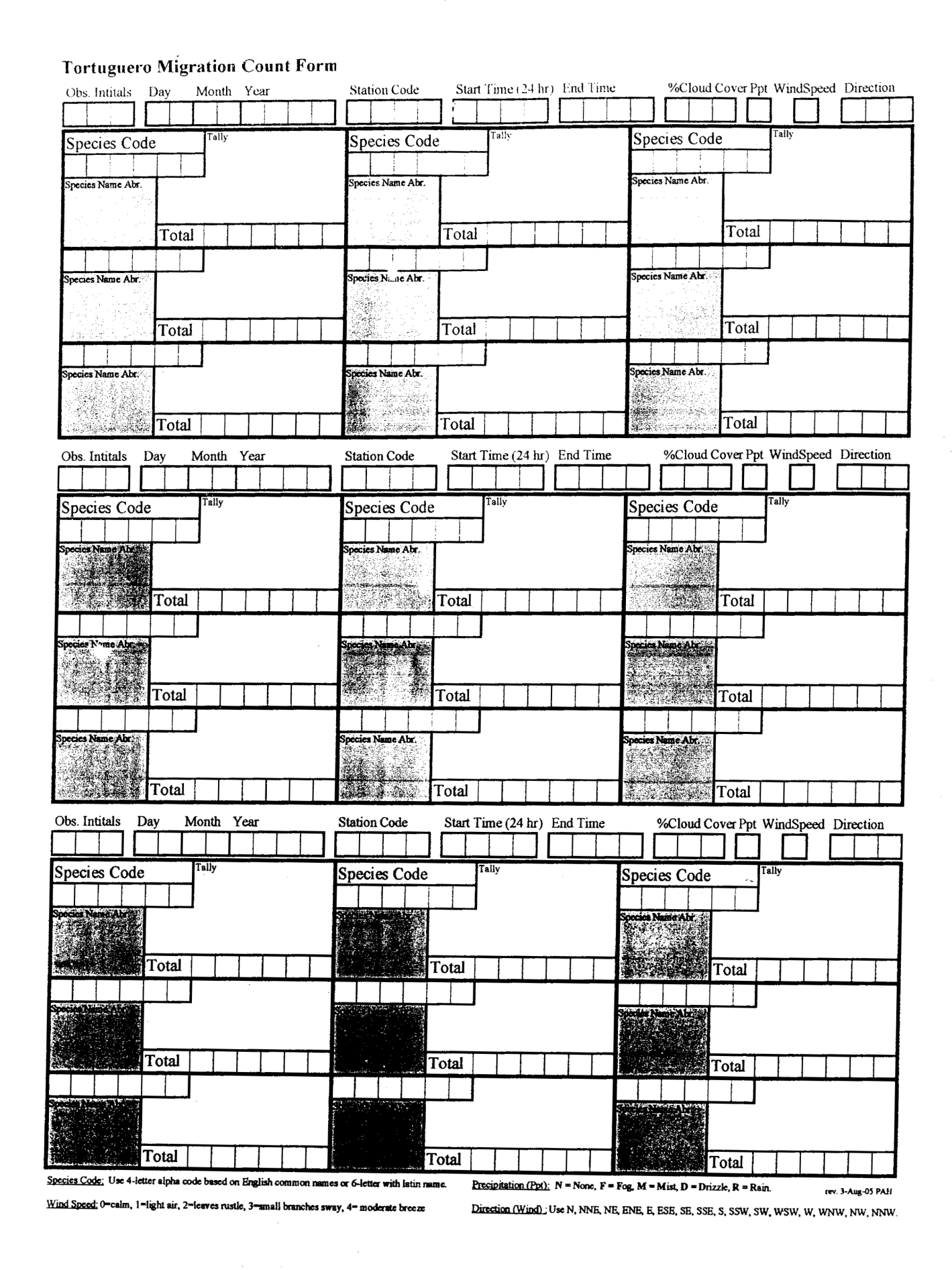
Thorup, K., I.A. Bisson, M. Bowlin, R.A. Holland, J.C. Wingfield, M. Ramenofsky, and M. Wikelski. 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. Proceedings of the National Academy of Sciences, U.S.A. 104:18115-18119.

Waugh, D.R., and C.J. Hails. 1983. Foraging ecology of a tropical aerial feeding bird guild. Ibis 125:200- 217.

Winkler, D.W. 2006. Roosts and migrations of swallows. Hornero 21(2):85-97.

## APPENDIX

**Protocol diurnal migration counts**

Protocol used for collecting data during diurnal migration counts with species and amounts observed, time and date, cloud cover, precipitation, wind speed and direction, and location.

1. [↑](#footnote-ref-1)