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DIVERSITY AND MOVEMENT PATTERNS OF PASSERINE BIRDS NEAR AN URBAN CENTER ON SANTA CRUZ, GALAPAGOS ISLANDS

A Thesis Presented

By

ANA MARIA GABELA

Submitted to the Graduate School of the
University of Massachussetss Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

May 2007

Graduate Program in Organismic and Evolutionary Biology

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DIVERSITY AND MOVEMENT PATTERNS OF PASSERINE BIRDS NEAR AN URBAN CENTER ON SANTA CRUZ, GALAPAGOS ISLANDS

A Thesis Presented

by

ANA MARIA GABELA

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Joseph S. Elkinton, Director
Program of Organismic and Evolutionary Biology

DEDICATION

To the Enchanted Islands….

And to the people who work to protect them from disenchantment…

ACKNOWLEDGMENTS

Although all this work is condensed into three years and a few typed pages much sweat, blood, and pain went into it, and it would not have been possible to complete with out the help and support from a lot of people spread all over the world. I would like to thank the SSM trail crew, Andrew Hendry, Mike Hendry, Luis Fernando de Leon, and Sarah Huber for 12 hour of grueling work. Thanks to all my field assistants that helped collect data and keept me sane: Luis Fernado de Leon, Jean-Sebastien Moor, Ken Gadow, Betty Mobbs, Kim Iwamoto, Emily Curd, Jessi Stitt, Brenda Whited. Morgan Jackson, Juan Carlos Valarezo, Matthew McFalls, Chris Niedel, Ian Taff, Katie Hallowel, Jessie Barker, and Amanda Whitton. Thanks to my "support staff" at CDRS: Matthew Simkins, Nel Beaumont, Paula Barnard, Graham Watkins, Alejandro and Alejandra Espinosa, and all of the CDF staff for all the encouragement. Thank you Team Pinzones 05-06. You make me proud!

Many thanks goes to the kind and patient people that helped me with the hardest part, writting, analysing, and re-writting my thesis. Thanks to my advisor, Jeff Podos and my committee, especially David Lahti for his endless patience and genuine interest for graduate students. Thanks for your statistical genius Ben Taft, Doug Sigorney, and Ted Stankowich. The OEB graduate students are a great resource of knowledge and support. Thanks for all your help! Natasha Taft rescued many of my maps and figures with quick lessons on illustrator. I would like to thank everyone that helped me get through the last couple of weeks of crunch time, specially the Podos lab, Dana Moseley, Ben Taft, David Hof, Kara Belinsky, and Elijah Goodwin for listening to my talk a few times more than they really wanted to. And everyone else that not only assured me everything was going

to go well but provided food, rides, and a few laughs when things got really chaotic, David McMartha, Annie Paradis, Zeke Nims, and Anna Soper.

Before I even arrived to Umass I felt I already knew Penny Jaques. She was the link to the OEB community and has always been available to help out in any way possible, from coffee to chocolates to more serious things like graduation requirements and employment issues. In the last year I have spent countless hours in Robbie Cairl office. Thanks for the conversation, the home-made meals, and the entertainment.

Jeff Podos kindly provided all the equipment necessary for this study, from mist-nets to endless roles of flagging. Additionally, Jeff Podos took care of all the permits necessary to conduct this study. Financial support from his National Science Foundation career grant IBN-0347291 covered most of this expedition's costs. Funding was also provided by Sigma Xi Grants-In-Aid of Research, Wilson Ornithological Society, E. Alexander Bergstrom memorial grant, and Animal Behavior Society. Equipment from Hi-Tec and Optics for the tropics was greatly appreciated. Assistance with travel logistics was provided by the Charles Darwin Reserach Station.

Most importnatly I want to thank my family, my Davidson family, my Biosphere family and all my friends. You guys were with me from the beginning, from painful lava transects, through all the re-writes and confusion, to the celebration. You deserve a degree for that too!

ABSTRACT

DIVERSITY AND MOVEMENT PATTERNS OF PASSERINE BIRDS NEAR AN URBAN CENTER ON SANTA CRUZ, GALAPAGOS ISLANDS

MAY 2007

ANA MARIA GABELA, B.S., DAVIDSON COLLEGE

M.S., UNIVERSITY OF MASSACHUSSETTS AMHERST

Directed by: Professor Jeffrey Podos

Many insights into ecological and evolutionary processes have come from studies of island systems. Diversity, abundance, and movement of species are restricted on smaller islands, but these dynamics can become increasingly complex as island size increases.

In recent decades urbanization and the human population on the Galápagos islands has increased rapidly, affecting wildlife in unknown ways. During 2005 and 2006, we sampled birds along a 4-km transect extending northeast of the city of Puerto Ayora, Santa Cruz Island. This allowed us to collect data on the potential impacts of rapidly growing urban center on passerine bird diversity and abundance. We also documented movement patterns of the medium ground finch (*Geospiza fortis*), the most abundant species on the transect, with a mark/recapture protocol. Although Darwin's finches have been an influential model for the last 150 years, little is known about their movements on larger islands.

Avian species diversity did not vary significantly along the transect from a periurban area into more remote habitat. Avian abundance, however, was inversely correlated with

distance from the urban center. This latter finding is consistent with a well-documented trend in urban ecology, in which periurban areas show higher abundance as compared to adjacent, less developed regions.

We also found recapture/re-sight rates for *G. fortis* within years were 7% and 11% in 2005 and 2006, respectively. The mean distance traveled by individual birds between recaptures or re-sightings was 430.4 m. The majority of movements were less than 500 m from the location of previous sighting. There was no relationship between the distance moved and the time between captures or re-sightings; birds were equally likely to move large distances over short intervals (days) as over longer intervals (years). There was no significant difference in movement distances between males and females. These data document the movement of *G. fortis* on a larger island. Further studies of gene flow among populations may provide further insight into the genetic and evolutionary consequences of movement patterns documented here.

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CHAPTER 1

DIVERSITY AND ABUNDANCE OF PASSERINE BIRDS AROUND AN URBAN CENTER ON SANTA CRUZ ISLAND, GALAPAGOS

Abstract

The Galápagos Islands provide a valuable opportunity to study the effect of recent urbanization on island wildlife populations. In recent decades the human population on the Galápagos has increased rapidly from 1,346 inhabitants in 1950 to 18,640 in 2001, affecting wildlife in unknown ways. During 2005 and 2006, we sampled birds along a 4-km transect extending northeast of the city of Puerto Ayora, Santa Cruz Island. Transect data and informal observations in the urban center allowed us to assess the potential impacts of a rapidly growing urban center on passerine bird diversity and abundance. We found that avian species diversity did not vary significantly along the transect, although it appears to be relatively diminished within the urban center. Moreover, we found that avian abundance along the transect was inversely correlated with distance from the urban center. This latter finding is consistent with a well-documented trend in urban ecology, in which periurban areas (immediately surrounding urban regions) show higher abundance as compared to adjacent, less developed regions. We hypothesize that human-related increases in avian abundance in periurban areas may portend future negative impacts on diversity as the intensity of urbanization continues. Further studies monitoring urbanization in the Galápagos are required to test this hypothesis and provide specific recommendations for the conservation of Galápagos avian species.

Introduction

Urbanization impacts wildlife in many ways, especially through the loss and degradation of habitat (Cam et al. 2000). By removing or altering natural habitats, urbanization is widely regarded as a principal threat to biodiversity (Clergeau et al. 1998). Many "specialist" species are unable to adapt to urban settings, and biodiversity is typically low in urban areas (Crooks et al. 2004; McKinney 2006). For example, forest interior birds and ground nesting birds are found in significantly lower densities in urban areas than in forests (Bessinger and Osborne 1982).

Urbanization does not impose negative effects on all species (Clergeau et al. 1998). Some species thrive in urban environments, while other species are found in numbers that exceed natural population sizes (McKinney 2006). Common examples of these species include pigeons (*Columba livia*), starlings (*Sturnus vulgaris*), and house sparrows (*Passer domesticus*) (McKinney 2006). These species effectively forage at bird feeders or make use of refuse associated with humans (Chace and Walsh 2006). These species also build their nests and rear their young in close proximity to humans. Urban areas have been considered "safe nesting zones" due to the absence of natural predators (Tomialojc 1982) despite the presence of cats, dogs, and corvids (Shochat 2004).

In periurban areas surrounding highly urbanized centers, bird diversity is usually higher than in urban centers, and sometimes higher than in non-urban regions ie. undisturbed habitats or those with minimal human impact (Jokimaki and Suhonen 1993; Clergeau et al 1998; Blair 1999; Blair 1996). Periurban locations may support relatively high

diversity and abundance of birds because they provide habitat for both native and introduced species (Blair 1996). This pattern has been documented for several well-established urban locations, but it is unknown if it holds for remote locations where urbanization is recent.

The urbanization of the Galápagos Islands of Ecuador has several distinct characteristics that provide a valuable opportunity to study several aspects of urbanization. The urbanization of the islands began in the early 20th century, but only in the last few decades has the human population increased significantly. The population on the archipelago in 1950 was 1,346, in 1974 it was 4,037, in 1990 it was 9,785, and in 2001 18,640 (www.inec.gov.ec). This provides us with the opportunity to study the effects of urbanization during its early stages. Urban areas in the Galápagos are projected to increase in density but not in area because further expansion is limited by national park boundaries. In addition the Galápagos Islands lacks the typical urban bird species found elsewhere on the mainland. Finally, an island population provides an unusual natural dynamic, insofar as islands support relatively few avian species, as compared to continental habitats. Thus it is unclear if patterns observed in other urban locations will occur in the Galápagos Islands.

In this study we focused on terrestrial birds in the vicinity of Puerto Ayora, Santa Cruz Island, the largest urban center of the Galápagos. We documented the diversity and abundance of bird species using a capture-release protocol undertaken at regular intervals along a transect that began in the periurban region and extended into an undisturbed

region. We also conducted informal observations of bird diversity (but not abundance) in the urban center.

We predicted that periurban regions of the transect would have higher species diversity and abundance than undisturbed areas on the transect further from town. This prediction is based on results from several studies (Jokimaki and Suhonen 1993; Clergeau et al 1998; Blair 1999; Blair 1996). Blair (1996), for instance, sampled 48 passerine species in and around Palo Alto, California, and showed that abundance and diversity peaked at intermediate levels of urbanization. Alternatively, bird diversity and abundance may be greater at more distant locations, suggesting that periurban environments have fewer food resources or nesting locations. Understanding how the Galápagos bird species are reacting to human activities including habitat encroachment may help us to provide guidance for their management and conservation.

Methods

Our study was conducted on Santa Cruz Island, Galápagos, Ecuador, from February through July of 2005 and 2006. For logistical reasons we conducted this study after the breeding season (December – Frebruary). A 4-km transect, within arid zone habitat, was established at the Charles Darwin Research Station (*Bahía Academia*) (GPS coordinates S 00˚44'15"-30": W 90˚18'05"-09"), which abuts the town of *Puerto Ayora,* and proceeded roughly northeast, toward *El Garrapatero* (GPS coordinates S 00˚40'20"–41'20": W 90˚13'10"–14'40") (Fig. 1). Intensive sampling of finches has been conducted at both *Bahía Academia* and *El Garrapatero* (e.g., Hendry et al. 2006), but not at

locations between these sites. Eleven sampling stations were placed at approximately 0.5 km intervals along the transect (Fig. 1). Sites labeled A and B in Figure 1.1 were considered to be within the periurban region of Puerto Ayora, whereas sites further from town were characterized by more natural conditions.

Transect stations A-J were sampled at least two separate times during this study, with each sample consisting of 1 - 4 days of netting. In 2005, birds were sampled at each sampling station for 5 - 17 days each. In 2006, birds were sampled at each sampling station for 11 - 14 days each. Variation in the number of days sampled during each visit to sampling stations was due to logistics. Transect station K was visited once, for 4 days, during 2005 only. For each day of sampling we opened between 4 and 9 mist nets (2.6 m high, and either 6 or 9 m in length) between 06:00 and 07:00 h, and closed them at approximately 11:00 h. On cooler days, additional sampling was conducted between 14:00 and 17:00 h. All nets were placed within 0.5 km of the day's sampling station. Most nets remained in the same location during the entire visit to one station. Occasionally nets were moved at the beginning of a day if no birds had been captured in the net the day before. We recorded the species and sex of all birds caught in each net, along with the time of day. We also noted the time nets were opened and closed in order to calculate standardized capture rates (birds/hr*m^2). Since both sampling effort and capture rate varied during each visit we pooled all sampling effort per sampling station and combined capture rate data for 2005 and 2006 into one capture rate per sampling station. We used linear regressions to evalutate abundance variation along the transect:

data were log transformed to meet the assumptions of normality. Avian diversity in town was noted through informal observations.

Results

We captured 4,683 individuals of 14 species during the two-year study: 2,567 birds in 2005, and 2,116 in 2006 (Table 1.1). Sampling effort was similar between years, with 44,861 hr*m^2 sampled in 2005 using 515 nets, and 59,635.hr*m^2 sampled in 2006 using 753 nets. The maximum number of birds captured at a single station was 785 at sampling station B.

The diversity of bird species captured was relatively uniform along the transect (Table 1.1 and Figure 1.2). Diversity, as measured by average number of species per locality ranged from 9.5 – 11.5 species, except for site K, which registered only 6 species. Only two species were noticeably absent from portions of our transect sample. No *Crotophaga ani* were captured at the distant end of the transect (stations H-K), even though they were seen there regularly, and *Coccyzus melacoryphys* were never captured or observed at stations closer to Puerto Ayora (stations A - D) (Table 1.1).

In contrast to relatively even diversity along the transect, we found noticeable spatial variation in abundance. Capture rates were highest near *Puerto Ayora*, and consistently low for all other sampling stations (Figure 1.3). The capture rate for the first two sampling stations (A and B) was 0.142 birds/hr*m^2 average for 2005 and 2006 combined, whereas the average capture rate for the remaining stations was 0.036 birds/hr*m^2 for

2005 and 2006 combined. Regressions of log transformed data show a significant decline in abundance with distance from town ($R^2 = 0.776$, $F = 27.642$, $P = 0.001$) (Figure 1.4).

Mirroring the interspecific data set, the abundance of *Geospiza fortis*, the most commonly captured species, was highest near *Puerto Ayora* (Appendix A). The average capture rate at stations A and B was 0.035 birds/hr*m^2 during the two-year study, while the average capture rate for the remaining stations was 0.009 birds/hr*m^2. This species showed a decline in abundance at more distant locations ($R^2 = 0.759$, $F = 25.217$, $P = 0.001$) (Appendix A). Other commonly captured species showed, a similar trend along the transect (Appendix A).

We observed very few species in the town of Puerto Ayora. Out of the 14 species observed on the transect we regularly saw only three within the town: *G. fortis, G. fuliginosa,* and *D. petchia,* with occasional sightings of *G. scandens*. Observations were generally made when food was available for the birds, which usually consisted of sugar, rice, or garbage. Due to the presence of food, the number of birds seen at any given time was high compared to that along the transect. Our informal observations are not sufficient to speculate about the abundance of birds in town.

Discussion

In our transect sample, we found that avian diversity was evenly distributed between periurban and more isolated areas. The diversity of sampled species was similar across all transect stations, except for the most distant station (K). This station was under-sampled

and thus provided an unreliable estimate of diversity. We never captured all 14 bird species at a single transect station. The greatest number of species captured at one sampling station was 11.5, 2.5 km from *Puerto Ayora*, (G). Differences in overall diversity along the transect were, however, minor. Crooks et al. (2004) found a different pattern in a study in costal southern California, in which higher bird richness was found in less disturbed habitat, as compared to urban-rural habitat. In our study, only *Coccyzus melacoryphys* appears to be limited to more natural areas, away from human settlements.

Our diversity results do not match our prediction that periurban sites would show higher avian diversity than at less disturbed sites, as has been shown in numerous other studies (Jokimaki and Suhonen 1993; Clergeau et al 1998; Blair 1996, 1999). Constancy in diversity across the transect suggests that urbanization on Santa Cruz Island is affecting avian populations differently than in mainland urban areas. Alternatively, perhaps urbanization has not yet had sufficient time to impose a discernable effect. This is plausible considering few urban ecology studies have been carried out in the tropics, and none have focused on sites that completely lack the typical urban species that are central to the trends observed in most urban areas. Puerto Ayora's early stage of urbanization may be the underlying cause of variation in patterns from those observed in other urban locations. Blair (1996) pointed out that although bird diversity appears to be highest in moderately urbanized areas, this may be due to the presence of exotic species. The lack of many exotic species in the Galapagos may have contributed to our results differing from other urbanization studies. It is also possible that as urbanization continues, bird diversity will decrease in general but peak in periurban sites, consistent with studies on

other localities. However, species diversity may remain evenly distributed if birds use periurban areas for specific purposes (such as feeding grounds) while maintaining a presence in less disturbed zones. This alternative seems plausible given the relative paucity of other passerine species that could compete for resources.

In contrast to periurban and natural habitats, our informal observations suggest that avian diversity is markedly reduced within the city. In the center of town we frequently observed *G. fortis, G. fuliginosa, D. petchia,* and occasionally *G. scandens,* but never saw any of the other 10 species of birds found along the transect. Although we were unable to quantify the abundance of birds in Puerto Ayora, the finch population in the town appears to be robust.

Abundance of birds, as measured by capture rate, was approximately four times higher at transect stations closer to town (stations A and B), compared to those found at more distant locations. Similarly, Crooks et al (2004) found high abundance of birds in the urban-rural habitat as compared to bird aboundance at locations farther away from urban areas. Transect stations A and B were near residences with bird feeders, bird baths, trash, and fresh water that provided supplementary resources for the birds, and likely attracted birds to the area. These types of resources are commonly found in periurban areas. Yet, areas that we now call periurban areas of Puerto Ayora could have historically been a location where higher abundance of birds were found even before the presence of urbanization. Beyond food supplements, these sites were generally wetter and greener, perhaps due to introduced vegetation. Counts of species on vegetation plots on the

transect found more species, species typically found in higher elevation, and more ground cover near periurban sites than in areas farther away on the transect(unpublished data). The abundance of vegetation in periurban areas may provide other food source for birds in periurban areas. Our findings suggest that birds are thriving on the outskirts of Puerto Ayora where they can benefit from the proximity to the human population and also have access to natural habitat (Blair 1996).

Our data set for individual species mirrored overall trends in population abundance. Past studies have found that birds that thrive in urbanized environments tend to be granivorous and/or insectivorous (Emlen 1974; Chace and Walsh 2006). Several of the species in this study are primarily granivourous (e.g., *Geospiza* species), and all feed to some extent on insects (Grant and Grant 1979; Grant 1999). *G. scandens* specializes on pollen of *Opuntia* cactii, but also feeds on small seeds and arthropods (Grant 1996). Granivores, insectivores, frugivores, and nectarivores may be more proficient at finding and utilizing food in proximity to humans (e.g. seeds and insects from weedy lawns and feeders and fruit and flowers from gardens) than other species. Some of the species that tolerate urban environments might also be more adept at avoiding urban predators such as cats and dogs.

This is the first study on the effects of urbanization on avian diversity and abundance in the Galápagos Islands. This study will serve as a baseline as urbanization continues to mature on Santa Cruz island. Other studies conducted in urban centers on other islands on the archipelago are needed to expand our knowledge of urbanization and aide in

conservation efforts at these sites. Human presence in the Galápagos Islands is affecting wildlife, as evidenced by the increased abundance of birds near human settlements. This effect may portend negative impacts for bird diversity in the natural habitat near urban centers. As urbanization continues to mature, habitat degradation may eventually lead to the reduction of avian diversity in areas beyond periurban areas. Even though the population and areas of urbanization are limited by the Galápagos National Park, it is evident that the population at least in Puerto Ayora is growing. Future studies will show whether avian diversity remains constant near human settlements or if these results are due to the present early stages of urbanization.

Tables

Table 1.1. Number of passerine birds captured, and their presence at sampling stations, along a 4-km transect running northeast of Puerto Ayora, Santa Cruz Island, Galápagos. Presence of at least one individual in 2005 or 2006 is indicated by an X, and absence by a 0.

			Presence or Absence										
Common Name	Scientific Name	Captures	A	B	C	D	E	F	G	H	I	J	K
Yellow warbler	*Dendroica petechia*	443	X	X	X	X	X	X	X	X	X	X	X
Galapágos mockingbird	*Nesomimus parvulus*	467	X	X	X	X	X	X	X	X	X	X	0
Galapágos flycatchers	*Myiarchus magnirostris*	746	X	X	X	X	X	X	X	X	X	X	X
Galapágos dove	*Zenaida galapagoensis*	4	X	X	0	X	0	0	0	X	0	0	0
Smooth billed ani	*Crotophaga ani*	6	X	0	X	X	X	0	0	0	0	0	0
Dark billed cuckoo	*Coccyzus melacoryphus*	11	0	0	0	0	X	X	X	X	X	X	0
Large ground finch	*Geospiza magnirostris*	72	X	X	X	X	X	X	X	X	X	0	0
Medium ground finch	*Geospiza fortis*	1152	X	X	X	X	X	X	X	X	X	X	X
Small ground finch	*Geospiza fuliginosa*	902	X	X	X	X	X	X	X	X	X	X	X
Cactus ground finch	*Geospiza scandens*	351	X	X	X	X	X	X	X	X	X	X	0
Woodpecker finch	*Cactospiza pallida*	20	0	X	X	X	0	X	X	X	0	X	0
Warbler finch	*Certhidea olivacea*	5	0	X	0	0	X	0	X	0	X	0	0
Vegetarian finch	*Platyspiza crassirostris*	292	X	X	X	X	X	X	X	X	X	X	X
Small tree finch	*Camarhynchus parvulus*	212	X	X	X	X	X	X	X	X	X	X	X
Total captures		4683											

Figure Legends

Figure 1.1. Location of the avian sampling transect on Santa Cruz Island, Galápagos, Ecuador. Distances of sampling stations along the transect were: A = 0 km, B = 0.4 km C = 0.5 km, D = 0.9 km, E = 1.5 km, F = 2.0 km, G = 2.5 km, H = 3.0 km, I = 3.4 km, J = 3.8 km, and K = 4.1 km.

Figure 1.2. Average number of species captured at each sampling station between 2005 and 2006. Number of species ranged from 9.5 - 11.5 excluding the sampling station at 4.1 km (K) which was relatively under-sampled and and only caught 6 species.

Figure 1.3. Plots of total avian capture rates for 2005 and 2006 combined versus distance along the transect. Error bars indicate standard error of the mean.

Figure 1.4. Linear regressions of the log transformed data of capture rate per sampling site. Capture rates for sampling station K was exculded for analysis. $R^2 = 0.776$, $F = 27.642$, $P = 0.001$, $y = -0.104x – 4.047$.

Figure 1.5. Plots of capture rates of nine bird species versus distance along the transect. Error bars indicate standard error of the mean.

Figures

Figure 1.1

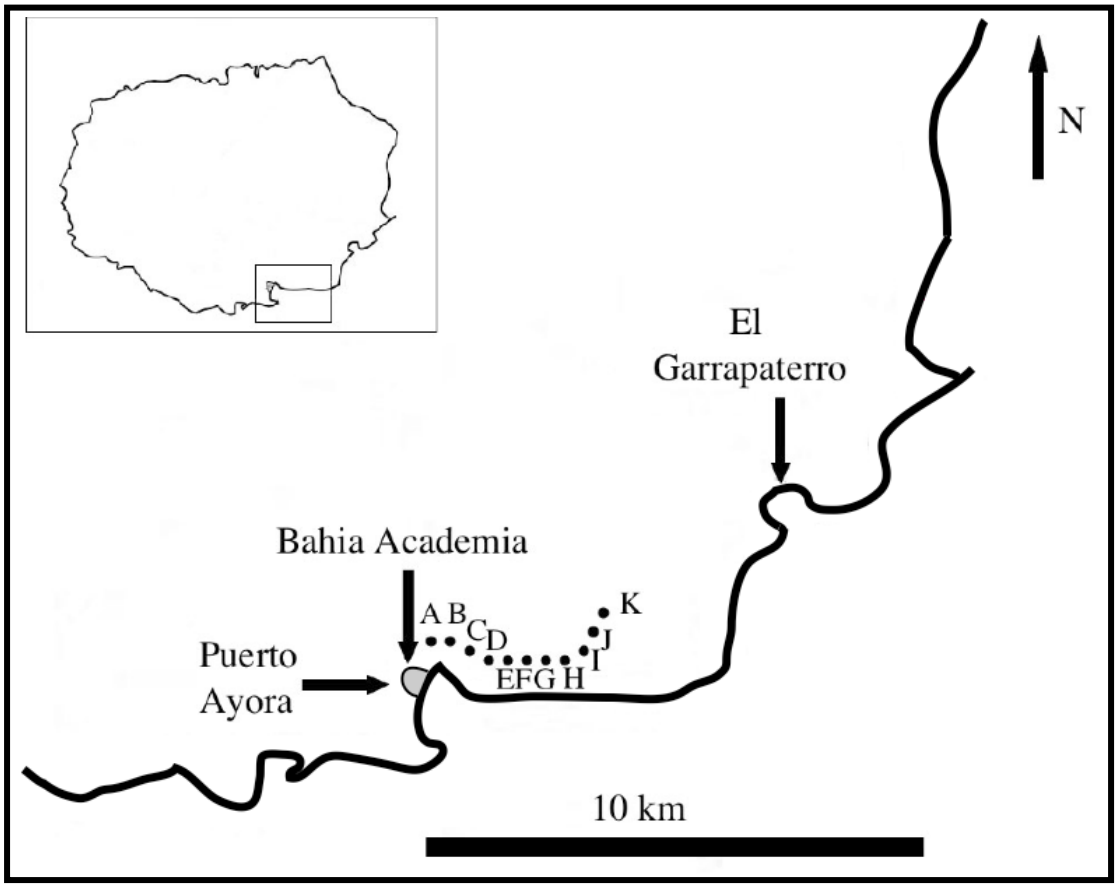

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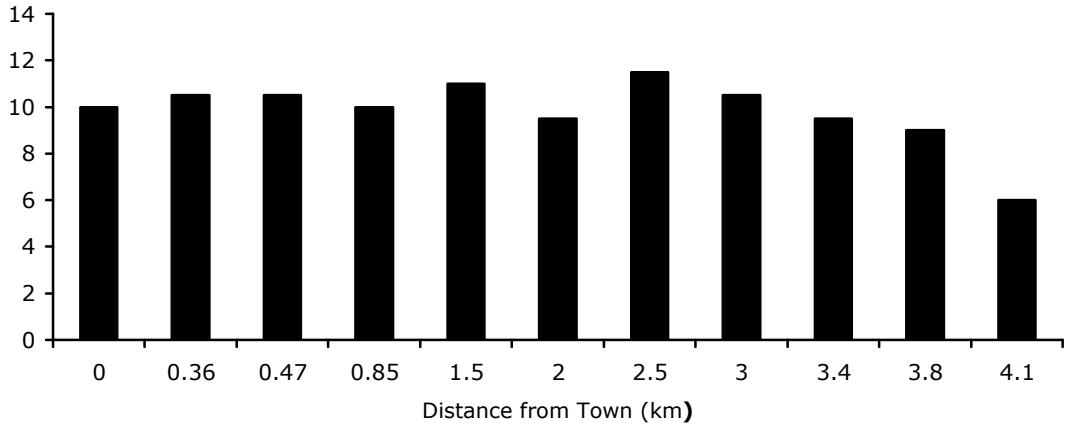
Figure 1.2.



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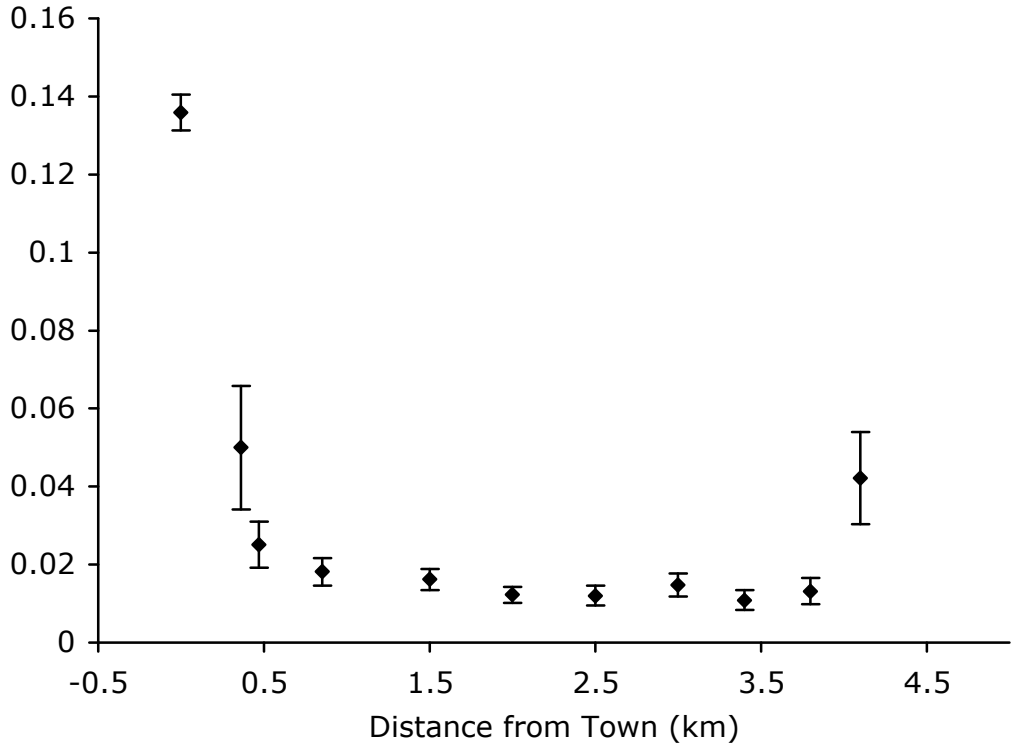

Figure 1.3. Plots of total avian capture rates for 2005 and 2006 combined versus distance along the transect. Error bars indicate standard error of the mean.

Figure 1.4.

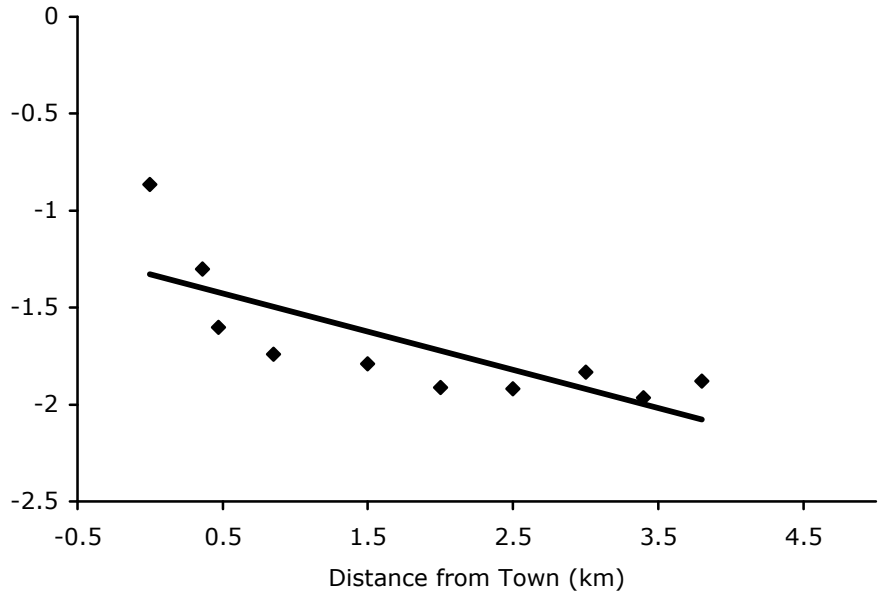

Figure 1.4. Linear regressions of the log transformed data of capture rate per sampling site. Capture rates for sampling station K was exculded for analysis. $R^2 = 0.776$, $F = 27.642$, $P = 0.001$, $y = -0.104x - 4.047$.

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Appendix A

Figure 1.5.

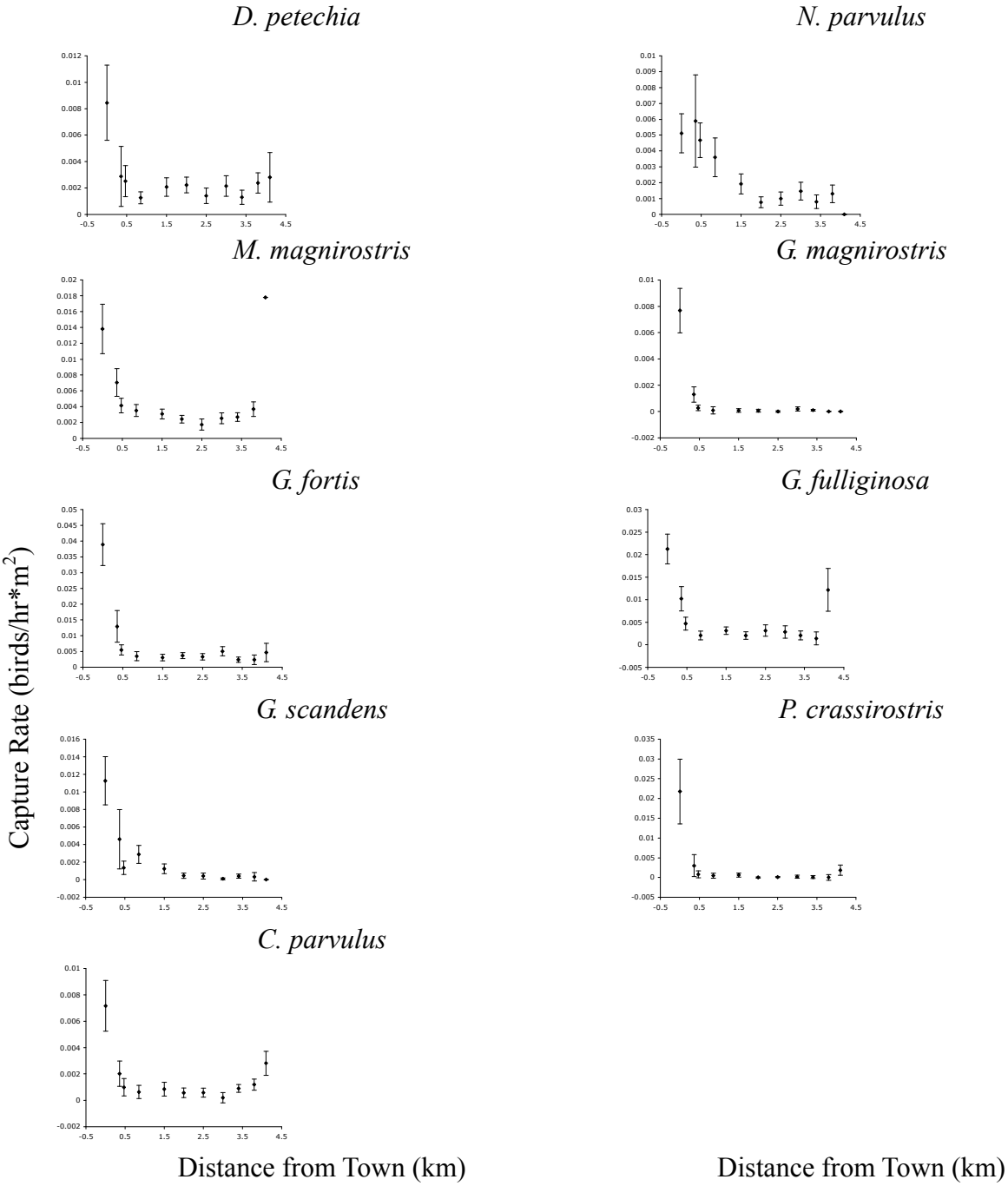

Figure 1.5. Plots of capture rates of nine bird species versus distance along the transect. Error bars indicate standard error of the mean.

Table 1.2. Linear regression equations of the log transformed data predicting capture rate based on distance of the sampling station from Puerto Ayora, Santa Cruz Island, Galápagos for the most commonly captured species.

	R^2	F	P	Equation
All Birds	0.776	27.64	0.001	y = -0.104x – 4.047
D. petechia	0.753	24.36	0.001	y = -6.217x – 0.071
N. parvulus	0.26	2.816	0.132	y = -0.60x – 6.308
M. magnirostris	0.69	17.81	0.003	y = -0.073x – 5.729
G. magnirostris	0.726	15.906	0.007	y = -1.92x – 8.704
G. fortis	0.759	25.217	0.001	y = -0.113x – 5.483
G. fuliginosa	0.656	15.264	0.005	y = -0.01x – 5.8
G. scandens	0.473	7.176	0.028	y = -0.146x – 7.211
P. crassirostris	0.694	13.609	0.01	y = -0.207x – 7.868
C. parvulus	0.634	13.858	0.006	y = -0.111x – 7.16

CHAPTER 2

MOVEMENT OF THE MEDIUM GROUND FINCH (*GEOSPIZA FORTIS*) ON SANTA CRUZ, GALAPAGOS

Abstract

Very little is known about the movement patterns of Darwin's finches on large islands, large enough for populations to become isolated from one another. At least two morphologically distinct populations have been identified on the larger island of Santa Cruz, Galápagos, Ecuador, with apparently little contact between them. This study aims to document patterns of movement in the medium ground finch, *Geospiza fortis,* in the southeast coastal region of Santa Cruz Island. We examined finch movement patterns along a 4-km transect between the two distinct populations using a capture-recapture/re-sighting protocol in 2005 and 2006. Recapture/re-sight rates within years were 7% and 11% in 2005 and 2006, respectively. The mean distance traveled by individual birds between recaptures or re-sightings was 430.4 m. The majority of movements were less than 500 m. There was no relationship between the distance moved and the time accrued between captures or re-sightings; that is, birds were equally likely to move large distances over short periods (days) of time than over longer time intervals (years). We did not find a relationship between the location along the transect and the distance moved, nor was there a significant difference in movement distances between males and females. Further studies of gene flow among populations on the island may provide further insight into the genetic and evolutionary consequences of movement patterns documented here.

Introduction

Many insights into ecological and evolutionary processes have come from studies of island systems. Islands often support fewer species than do continental areas of equivalent size. This facilitates the study of ecological processes such as interspecific interactions (e.g. Grant and Grant 2006). Significant seasonal or annual ecological fluctuations on islands enable researchers to document evolutionary processes such as natural selection that are linked to ecological variation. These processes tend to occur more rapidly on islands than in continental areas. Islands also often comprise closed populations, with little inter-island migration, thus facilitating the study of population level processes. Yet, as islands increase in size the degree of complexity of these processes may increase as well. Larger islands have more space and tend to have more species and more individuals of these species. Large islands can also have multiple vegetation zones, thus providing a more diverse array of habitats on which organisms can specialize. Spatial movement are restricted on smaller islands, but can play increasingly influential roles as island size increases, for instance as organisms adapt to distinctive microhabitats or become isolated from one another.

This study documents patterns of movement in a species of Darwin's finch (*Geospaiza* fortis)on the large island of Santa Cruz on the Galápagos Islands (~ 1000 km^2). Darwin's finches have served as an influential model system in ecology and evolutionary biology for over 150 years (reviewed by Grant 1999). Yet most of the information that is available about movement patterns in Darwin's finches has emerged exclusively from studies of

populations inhabiting small islands (e.g., Daphne, ~ 0.32 km^2Grant 1999), or inhabiting restricted locations such as around Darwin Bay on Genovesa Island (Grant and Grant 1989) or at *El Garrapatero,* Santa Cruz Island (Podos 2007). On small, isolated islands, site-fidelity is naturally very high. Some evidence for high site-fidelity comes from the large cactus finch (*G. conirostris*) on Genovesa Island, in which natal dispersal was shown to be less than 600 m, and females that re-paired in one mating season did not move more than one territory (Grant and Grant 1989). Similarly, on Daphne Island, individual birds tended to remain in the same vicinities from one year to the next (L. Keller, personal communication). Moreover, very few birds are thought to immigrate to or emigrate from Daphne, relative to the base population size (Grant 1999). Occasionally finches fly between islands, as inferred through analysis of genetic relationships among populations (Petren et al. 2005). Support for this inference also comes from anecdotal observations of birds flying between islands (Grant 1999). Although finches fly long distances on occasion, and at least once the 1000 km required for colonization, some 2-4 million years ago, we do not know how far birds move on a regular basis on larger islands. At restricted localities it is possible to evaluate the number of birds and movements that remain on site from year to year, although it is not possible to assess distances moved by birds that do not remain on site.

Movement within larger islands or across more expansive field sites is difficult to study due to challenges in logistics and in distinguishing between migration and mortality in the absence of recaptures or re-sightings. Nevertheless, movement patterns within larger islands are worth closer evaluation for at least two reasons. First, it is not clear whether

population processes on small islands, which have been particularly well documented (e.g., Grant 1999, Grant & Grant 2002), necessarily mirror those on large islands. Within-island divergence, for instance, may be more likely on larger islands, because of greater opportunities for geographic isolation (Kleindorfer et al. 2006). Second, large islands support substantially larger finch populations than do small islands, and the evolutionary and ecological processes therein may thus be more representative of general trends for the species. Increased species diversity on larger islands may, for instance, facilitate rapid evolution through greater selective pressure from interspecific competition.

The present study was motivated by the discovery of two morphologically distinct "populations" of the medium ground finch, *Geospiza fortis* on Santa Cruz Island, the second largest of the archipelago. These populations, separated by only about 11 km, show clear differences in patterns of beak size variation. More specifically, a population at *El Garrapatero* has two distinct beak sizes (bimodal), whereas the population at *Bahía Academia* appears to be unimodal (Hendry et al. 2006). Furthermore, the birds at *El Garrapatero* respond weakly to playbacks of songs of birds from *Bahía Academia*, as compared to responses to playback of songs from the local site (Podos 2007). This suggests that birds at *El Garrapatero* are familiar with songs from their own site, but not with songs from *Bahía Academia* (Podos 2007). We have banded since 1999 at *Bahía Academia* and since 2003 at *El Garrapatero*, and only one bird of the ~500 banded birds at *Bahía Academia* or at *El Garrapatero* have been recaptured or re-sighted at the other site (Podos 2007). Recapture rates at the two sites are distinct and range from approximately 22 - 29% at *El Garrapatero*, (unpublished data), to 3 - 5% at *Bahía*

Academia. These lines of evidence suggests a recent history of limited gene flow among the populations, which in term might be attributed, at least in part, to low dispersal between these sites.

To measure movement patterns of *G. fortis* along southeastern Santa Cruz Island, we used a capture-recapture protocol, conducted along a 4-km sampling transect. The transect originated at the Charles Darwin Research Station (CDRS) in *Bahía Academia*, and headed east-northeast towards *El Garrapatero*. Captures and recaptures/re-sighting attempts were conducted at regular intervals along the transect over a two year period. We documented the locations of recaptured or re-sighted individuals, and calculated the distance traveled by each individual during the intervening time frame. The capture-recapture protocol is one of several possible methods for assessment of movement patterns, and has some intrinsic limitations. For instance, with this method it is not possible to distinguish among movements within a birds' typical territory or home range, to the extent that such territories or home ranges exist, as compared to more long-distance movements of a more permanent nature. Other methods, such as radio-tracking, would be preferable towards this end. Nevertheless, the method employed is particularly suitable for the difficult field conditions encountered in the Galápagos, and for obtaining a snapshot of movement patterns for as large a sample size possible within the time frame of the study. Our transect data allow us to answer questions about three aspects of finch movements (1) how far do birds move? (2) do birds move larger distances over larger periods of time? (3) do birds tend to move in particular directions? (4) is there a

relationship between distance moved and the previous location birds from where birds were observed? (5) do males and females differ in patterns of movement?

Methods

Study site and data collection

Our study was conducted on Santa Cruz Island, Galápagos, Ecuador, February through July of 2005 and 2006. We conducted this study after the breeding season (December – February) when movement patterns would be more typical and not restricted to finding a mate, nest building, or feeding offspring. A 4-km transect, situated entirely within arid zone habitat, that is the prefered habitat for *G. fortis*, was used for sampling. The transect began at the Charles Darwin Research Station (CDRS) (GPS coordinates S 00˚44'26.1": W 90˚18'09.0"), which abuts the town of *Puerto Ayora,* and proceeded roughly east-northeast in the direction of *El Garrapatero* (GPS coordinates S 00˚40'20"–41'20": W 90˚13'10"–14'40") (Fig. 1). The transect followed roughly the contour of the coast (Figure 2.1). Intensive sampling of finches had been conducted at both *CDRS* and *El Garrapatero* (e.g., Hendry et al. 2006), but not at locations in between. Sampling stations were marked at approximately half-kilometer intervals along the transect. Our study included a total of 11 sampling stations, labeled A-K (Figure 2.1). Additional sampling and observations were made at CDRS locations (W-Y) and at sampling station Z, which was near but not on the transect.

Transect stations A-J were sampled at least two separate times during each year of the study, with each sample consisting of 1-4 days of netting. In 2005, birds were sampled at each station for 5-17 days each. In 2006, birds were sampled at each station for 11 - 14 days each. Transect station K was sampled once, for 4 days, during 2005 only. For each day of sampling we opened between 4 and 9 mist nets (2.6 m high, and either 6 or 9 m in length) between 06:00 and 07:00 h, and closed them at approximately 11:00 h. On cooler days, additional sampling was conducted between 14:00 and 17:00 h. All nets were placed within the day's sampling station area within a 180 m radius from each other. The location of all nets and captures were noted using a GPS. Additional captures off the transect at X and Ywere made using potter traps.

Our study focused on *G. fortis*, by far the most abundant bird in the study area (Chapter 1). We fitted all *G. fortis* with a numbered metal leg band and unique combinations of three colored leg bands, to aid later identification. The identity of all birds recaptured or re-sighted and locality was recorded. Re-sightings were documented on the basis of band combinations and were made opportunistically. Birds captured multiple times at a given locality during a given sampling period were not considered "recaptures". Moreover, our analyses included recaptures of birds originally banded at *Bahía Academia* prior to the start of this study (between 2002-2004) if the precise original capture sight had been noted.

Statistical analyses

Our first set of analyses quantified overall patterns of movement along the transect. We calculated means and standard deviation of distances traveled between capture and recapture/re-sighting events. If a bird was recaptured or re-sighted multiple times, distances were calculated from the previous location. Next we used linear regression analysis to assess whether distance traveled between capture and recapture/re-sighting events corresponded to the time passed between those events. We predicted that birds would move larger distances over longer time periods.

Second, we assessed whether distance of movement corresponded with the site of the prior capture or sighting locality. Given variation in the proximity to human settlement at the beginning versus the end of the transect (Figure 2.1; Hendry et al. 2006), we predicted that distances moved would vary along the transect. To test for this variation, we categorized recapture/re-sighting events into three categories; those for which the preceding capture/sighting event had been made around stations A-C (proximate), those around stations D-F (middle), and those around stations G and beyond (distant). Subsequent distances moved were compared statistically among categories using a Kruskall-Wallis non-parametric test. If a bird was recaptured or re-sighted multiple times, all movements were used for the analysis of distance moved and each subsequent recapture or re-sight was analyzed from the previous location.

Finally, we compared the movement patterns of females versus males separately to test for the presense of significant differences between the sexes and between years. Prior studies in other passerines have demonstrated that females tend to move greater distances

than males (Shields 1984). We calculated the recapture/re-sight rate per year for males and females. We also calculated means and standard deviation of distances traveled by males and females between capture and recapture/re-sighting events and tested for differences using a two-tailed t-test assuming equal variance.

Results

Recapture/re-sighting Data

We banded 1171 *G. fortis,* of which 94 were recaptured/re-sighted at a later time (Table 2.1.). Of these birds, 27 were re-sighted. Additionally we recaptured/re-sighted 12 birds that had been banded in 2004 or earlier, prior to the onset of this study. In 2005 we banded 671 *G. fortis* of which 43 were recaptured or re-sighted. Eight other birds were recaptured/re-sighted but had been banded before 2005. In 2006 we banded 500 birds of which we recaptured or re-sighted 55 and 4 birds banned before this study began. Only 3 birds recaptured or re-sighted during both years had been banded prior to this study.

Movements along the transect

The mean distance moved by all recaptured/re-sighted birds in this study was 430.4 $\pm$ 639.5 m (SD, N = 115) (Table 2.2). Distances moved varied among years; in 2005 the mean distance moved by all recaptured/re-sighted birds was 284.3 $\pm$ 355.4 m (N = 56), and in 2006 was 569.1 $\pm$ 802.4 m (N = 59). Excluding recaptures/re-sights of bird banded in previous years, the mean distance moved by birds banded and recaptured/re-sighted within 2005 was 246.6 $\pm$ 343.6 m (N = 48), and in 2006 was 555.1 $\pm$ 772.2 m (N = 17). The mean distance moved by birds banded in 2005 but recaptured in 2006 was 628.3 $\pm$

848.4 m (N = 38). The maximum distance moved by birds recaptured in 2005 was 1600 m while in 2006 it was 3200 m (Table 2.2).

The majority of recaptures/re-sightings (78 of 115) occurred within 500 m of the previous capture sight (Table 2.3 and Figure 2.2). Only 16 of 115 movements exceeded 1 km (Table2. 3 and Figure 2.2). All three birds that were recaptured both in 2005 and 2006 were re-sighted at the same sampling station as originally captured, moving only 0-60 m from the site of previous capture. One bird recaptured multiple times moved a distance of 313 m.

Rate of movements on the transect

In the two years of this study there were few movements exceeding 1 km. Some of the few birds that were found to move over 1 km did so in a few days, although the very largest movements that were recorded along the transect were of birds that had been observed approximately a year earlier (Figure 2.3). Yet the few birds that were recaptured after 3 or 4 years moved less than 500 m from the site of original capture (Figure 2.3). In 2006, there was a greater incidence of shorter ($\leq$ 500 m) movements than in 2005 (χ^2 0.156 df =1, N = 115, P > 0.05). The average rate of movement of birds banded and recaptured/re-sighted during this study was 9.7 $\pm$ 65.5 m/d (N = 115). The average rate of movement of birds banded and recaptured/re-sighted in 2005 was 0.99 $\pm$ 2.1 m/d (N = 48). The average movement rate of birds banded in 2005 but recaptured/re-sighted in 2006 was 4 $\pm$ 6.9 m/d (N = 38). The average rate of movement of birds banded and

recaptured in 2006 was 53 $\pm$ 167.7 m/d (N = 17). The higher rate in 2006 is strongly influenced by one bird that moved 2100 m in 3 days with a rate of 700 m/d.

Movement tendencies on the transect

Recaptures/re-sights of birds originally captured at the same station were found at every sampling station both in 2005 and 2006 (Figure 2.4). The exception was sampling station K, where no birds banded there were recaptured/re-sighted during the brief sampling period spent there or elsewhere along the transect. Approximately half of the recaptures/re-sights during both years were of birds within the same sampling station as the one in which they were previously captured or observed (30 out 56 in 2005 and 30 out of 59 in 2006). The most movements between sampling station occurred between the first three sampling stations (A-C) and locations on CDRS (W-Y) (32 out of 44 total, 21 of 26 in 2005 and 11 of 18 in 2006) (Figure 2.4). This pattern was statistically significant (χ^2 0.001 df = 1, N = 55, $p > 0.05$). On the other hand, in 2006 there seemed to be more movements towards more distant sampling stations on the transect (Figure 2.4), although this pattern was not statistically significant (χ^2 0.07, df = 1, N = 52, $p > 0.05$). We did not find a significant pattern between the distance birds moved and the location previously captured or observed ($\chi^2 = 3.516$, df = 2, P = 0.172) (Figure 2.5). Yet, in 2005 we found a strong trend for birds captured at proximate sampling stations (A – C) to moved greater distances between recapture or re-sighting than birds found initially at other sampling stations. This trend was not statistically significant ($\chi^2 = 5.588$, df = 2, P = 0.061) and was not found in 2006 ($\chi^2 = 3.028$, df = 2, P = 0.22).

Sex Specific Patterns of Movement

Of the 106 birds recaptured/re-sighted in this study, 61% were males. Juveniles look like adult females and therefore the estimated number of females recaptured/re-sighted includes juveniles. Of the 51 birds recaptured in 2005, 26 (51%) were males, and 25 (49%) of these birds were females. Of these birds, 1 male was originally captured in 2002, 1 female was banded in 2003, and 2 males and 4 females were originally banded in 2004. All other recaptures were of birds banded in 2005. In 2006 out of the 55 the birds recaptured, 16 (29%) were females and 39 (71%) were males. Of these birds, 1 female was originally banded in 2003, 2 males and 1 female were banded in 2004, and 26 males and 8 females were banded in 2005. The rest of the recaptured birds were of banded birds in 2006. Only 3 birds were recaptured in 2005 and 2006, 1 male and 2 females. The mean distance moved by males during the two year study was 416.5 m $\pm$ 609.7 m and the mean distance moved by females was 467.6 $\pm$ 701.6 m ($t = -0.4$, $df = 113$, $p = 0.684$). The mean distance moved by males in 2005 was 285.4 $\pm$ 360.9 m ($N = 31$), and the mean distance for females was 282.9 $\pm$ 355.9 m ($N = 25$). The mean distance moved by males in 2006 was 511 $\pm$ 728.9 m ($N = 43$) and the mean distance moved by females was 756.3 $\pm$ 982 m ($N = 16$). The mean distances moved by females and males were not significantly different either year ($t = 0.026$, $df = 54$, $p = 0.98$ for 2005, $t = -1.04$, $df= 57$, $p = 0.302$ for 2006) (Table 2.2).

Discussion

Recapture/re-sighting data

In this study, we banded 1171 *G. fortis* and 94 were either recaptured or re-sighted again at a later time. Recapture/re-sight rate for the first year of this study was 7.6%, and

improved to 11% for the following year. This slight increase might be attributed to a greater percentage of the population having been banded from the prior year's efforts. Some studies in other passerine species have found higher rates of recapture, although over less dispersed sampling sites. Takagi (2003), for example, found recapture rates between 6-23% in bull headed shrikes. Diquinzio (2001) found a mean return rate for adult saltmarsh sharp-tailed sparrows to be of 35.1% over a 5-year study. Our recapture rate is higher than conservative recapture estimates from *Bahía Academia* which ranged from 3 – 5% but lower than recapture rates at *El Garrapatero*, which ranged from approximately 22 - 29% between 2004 - 2005 (unpublished data). Most capture - recaptures studies have limitations on detecting birds that leave the study site; our study covered a larger area potentially allowing us to recapture/re-sight individuals that move larger distances. These are the first data documenting movement patterns of *G. fortis* over a relative large spatial scale.

Movements along the transect

Since 2003, when we started banding *G. fortis* at *El Garrapatero* only one banded bird from *Bahía Academia* has been found at *El Garrapatero*. This is the longest movement ever recorded for an individual Darwin's finch, and the first indication that these birds will move ~11 km within an island. Moreover this suggests that birds are, at least on occasion, willing to move to a morphologically distinct population, from a population with a unimodal beak size distribution at *Bahía Academia* to a bimodal population at *El Garrapatero*. To date no bird has been found to move in the opposite direction, from *El Garrapatero* to *Bahía Academia*. Despite this unique case of large movement, the present

study found few individual large movements. The majority of the movements were $\leq$ 500 m, and the mean distance moved was 430.4 $\pm$ 639.4 m. The mean distance moved by birds varied somewhat between years, with larger distances found in 2006. Although these birds are certainly able to move large distances, they seem to move shorter distances more often.

Different movement patterns across years could occur as a response to variation in precipitation and its effect on the availability of food. It is useful to note that the precipitation, an important factor in the breeding cycle of *G. fortis*, varied between years. In January – July, nearly twice the precipitation was recorded in 2005 (144.70 mm) than in 2006 (82.60 mm). Although there was less precipitation in 2006 it was evenly spread out through out the season. 2005 was characterized by an intense drought followed by heavy rains as in 2005. Both droughts and the period following the first rains are difficult times for granivorous birds as there is less food available either due to the drought or because the seeds are germinating after the rain. This may prompt birds to move larger distances looking for food.

Rate of movements on the transect

We expected birds to move larger distances over longer periods of time along the transect, based on the simple expectation that longer periods of time would provide more opportunity for birds to move. Yet we found no significant relationship between distance moved and the time delay between banding and recapture or re-sight (Figure 2.3). We found a higher overall movement rate for birds in 2006 (53.0 $\pm$ 167.7 m/d, N = 17). The

higher movement rate in 2006 is partially due to one bird that moved 2100 m in 3 days (Figure 2.3). This could be an effect of being captured that leads to birds moving large distances to avoid being recaptured. This was was only seen in a few birds. More birds moved short distances following their capture (Figure 2.3). Birds that had a full year between banding and recapture moved at a rate of 4.0 $\pm$ 6.9 m/d, N = 38 (birds banded in 2005 but recaptured in 2006). Birds that moved over 1 km did so in 3 - 99 days or over a full year. The largest movement was of 3200 m and occurred in 333 days. These birds seemed equally likely to fly large distances in a few days or a full year.

Movement tendencies on the transect

The high number of recapture/re-sights at the same sampling stations where birds were originally captured suggest a large number of *G. fortis* are sedentary. We predicted that the movement patterns might be affected by the presence of the human settlement, Puerto Ayora, near sampling stations A - B. In 2005 there was a statistically significant pattern in which more movements occurred nearest to Puerto Ayora (between sampling stations A-C). In the second year of the study we observed more movements farther along the transect (sampling stations E-J), but this pattern was not statistically significant. The distance traveled by birds originating from different parts of the transect were not statistically significant either. We did not find a clear pattern in the direction of movement or distance of these movements along the transect. This suggests that there is no "seasonal migration" or joint movements toward or away from any areas of the transect during February – July. If this were the case our sampling would have been able

to detect such movements. Annual effects may be better detected, however, when comparig with more severe droughts or more intense rains, such as El Nino years.

Sex specific patterns of movement

Differential dispersal between males and females birds is common in birds. In species where one sex must establish and defend a territory, that sex tends to be highly site-faithful (Greenwood 1980; Payne and Payne 1993). In the case of most passerines, males defend territories and females are more likely to disperse and travel farther than males (Shields 1984). Male *G. fortis* defend a mate and a territory during the breeding season. Although we caught more males than females, we did not find a statistically significant difference in the distance moved by males and females. This may indicate that there is no difference in movment patterns in *G. fortis* between males and females. But it is worth noting that juvenile males look like females until they molt into breeding plumage. Thus, it is possible that several of the females identified during this study were indeed juvenile males. There were 6 cases in which recapture the individuals originally identified as females had molted into breeding male plumage. For this reason we are unsure if our data regarding female recaptures are accurate. More males than females banded in 2005 were recaptured in 2006. It is unclear if this is due to higher survival of males or not.

Conclusion

Little is known about movement patterns of Darwin's finches on larger islands. This study provides data regarding the movement patterns of *G. fortis* on the southeastern side of larger island of Santa Cruz. Based on the findings of Podos (2007) and Hendry et. al

(2006), Santa Cruz Island appears to support at least two morphologically distinct populations of *G. fortis*, found at *El Garrapatero* and *Bahía Academia*. In this study we did not find evidence indicating signficant movement between these two populations. Yet, a few birds in this study moved almost the maximum distance we sampled suggesting that if we had sampled a larger area we might have found birds that moved even larger distances. This indicates that contact between the two populations is likely. It would be intresting to know if there is also gene flow between. So far we have only observed limited movement between the two populations which may allow these two populations to evolve along differing trajectories. The populations are not separated by a geographical barrier. Yet as the Galápagos Islands face year-to-year variation in environmental factors, e.g. via increasingly strong El Niño or La Niña events, these populations may face intense divergent selection pressures which may cause them to differentiate much faster than predicted, and possibly to a degree that can lead to speciation. DNA analysis of the populations at *Bahía Academia*, *El Garrapatero*, and on the transect may provide further insight into the genetic and evolutionary consequences of movement patterns documented here.

Tables

Table 2.1. Total numbers of captures and recaptures for 2005 and 2006. Number of recaptures in 2005 and 2006 by year of original capture.

	2005	2006
Released	671	500
Recaptured	51	55
Recapture Rate	0.076	0.11
Original Capture		
2002	1	0
2003	1	1
2004	6	3
2005	43	34
2006	N/A	17

Table 2.2. Summary of distances moved for all birds, females, and males recaptured in 2005 and 2006.

	2005			2006		
Distance (m)	All Birds	Females	Males	All Birds	Females	Males
Minimum	0	3	0	0	0	16
Maximum	1600	1100	1600	3200	3000	3200
Mean	284	283	285	569	756	511

Table 2.3. Number of movements by distance for 2005 and 2006.

Distance Moved Meters	2005 Number of Birds	2006 Number of Birds
0	2	3
1—10	3	0
11--20	3	5
21-30	2	5
31-40	3	1
41-50	5	4
51-60	1	1
61-70	2	2
71-80	3	3
81-90	1	2
91-100	2	0
101-200	7	5
201-300	2	2
301-400	6	2
401-500	0	2
501-600	5	3
601-700	1	4
701-800	3	0
801-900	0	0
901-1000	2	3
1100	2	4
1200	0	1
1500	0	2
1600	1	0
2100	0	1
2600	0	1

Figure Legends

Figure 2.1. Map of study sites on Santa Cruz Island, Galápagos Ecuador. Letters indicate sampling stations along the transect. Linear distances from site A were measured, using a GPS unit, as follows: A (0 km), B = 0.36 km, C = 0.47 km, D = 0.85 km, E = 1.5 km, F = 2.0 km, G = 2.5 km, H = 3.0 km, I = 3.4 km, J = 3.8 km, K = 4.1 km, Z= 0.70 km.

Figure 2.2. Distance moved by birds for 2005 and 2006.

Figure 2.3. Distances moved for all recaptured/re-sighted birds in 2005 and 2006. $y = 0.134x + 407.42$, $R^2 = 0.0024$.

Figure 2.4. Movement Diagrams. Diagram shows direction of movement between sampling stations for 2005 and 2006. All arrows indicate one bird moved in that direction. In 2005, 5 arrows represent 2 birds, 3 arrows represent 3 birds, 1 arrow represents 4 birds, 2 arrows represent 5 birds, and 1 arrow represents 6 birds. In 2006 10 arrows represent 2 birds, 2 arrows represent 3 birds, 2 arrows represents 4, and 1 arrow represents 6 birds. In both years the arrows that represent the most number of birds (2005 4-6 and 2006 3-6 birds) were all recaptures at the same sampling station.

Figure 2.5. Plot of Kruskal-Wallis analysis. Sampling stations were grouped into proximate (A – C), middle (E – F), and distal (G –J). $\chi^2 = 3.516$, df = 2, P = 0.172.

Figures

Figure 2.1.

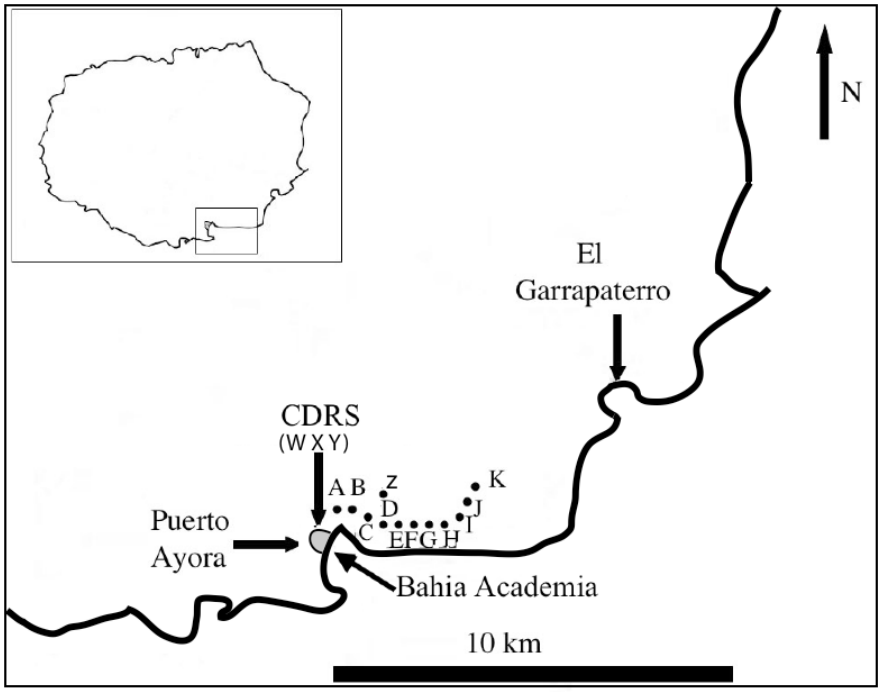

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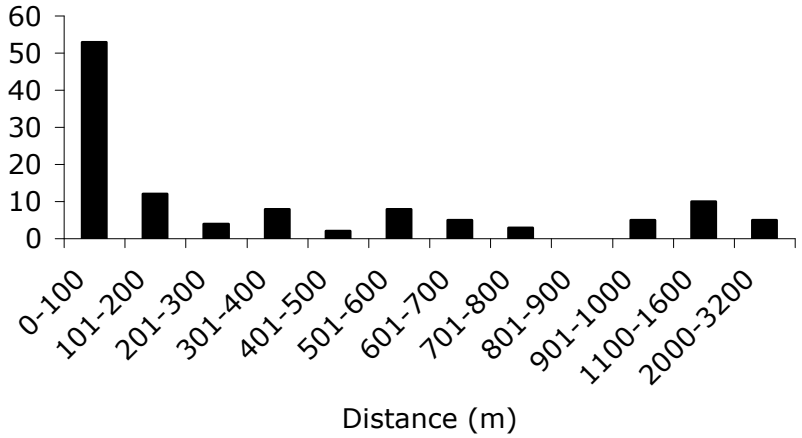
Figure 2.2.



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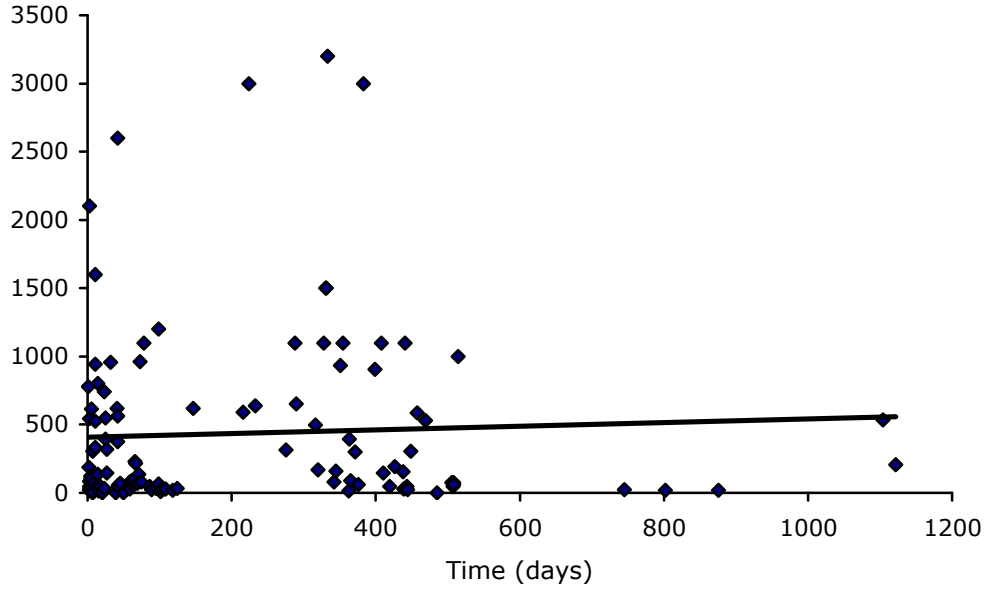

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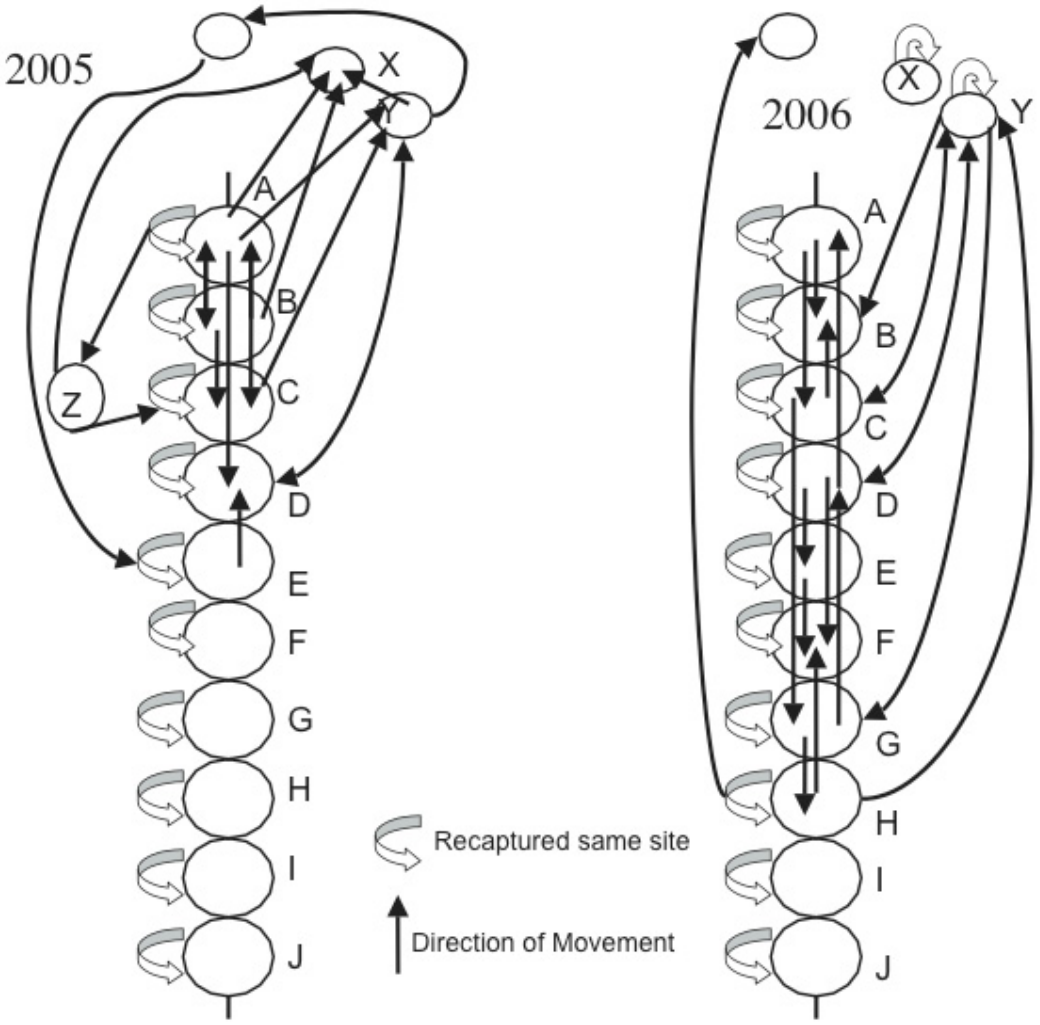

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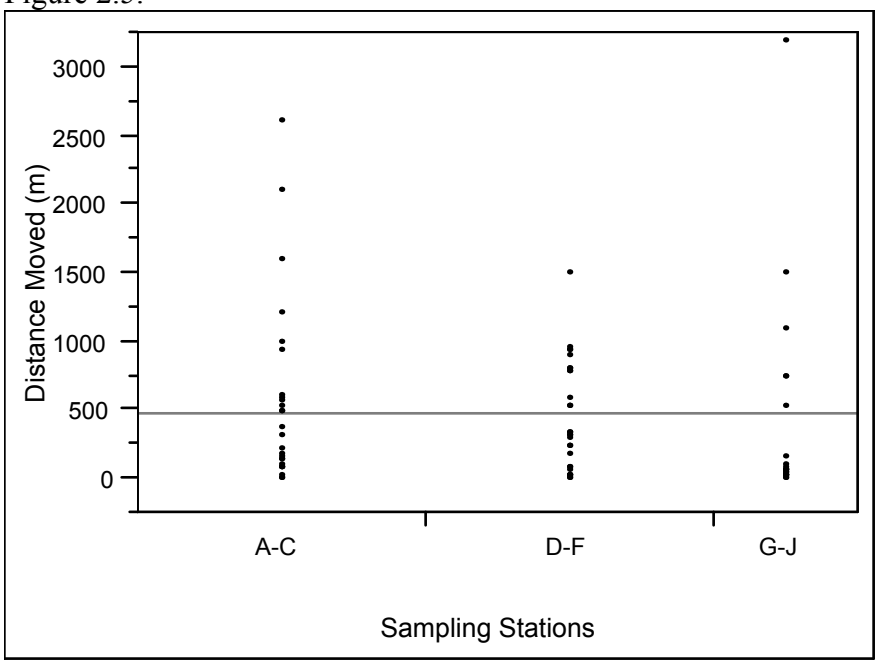

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