

ASPECTS OF FORAGING IN BEES: APPLE POLLINATION, NATIVE BEE
POPULATIONS, AND HONEY BEE COMMUNICATION

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

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August 2006

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Cornell University 2006

Bees are well known for their ability to pollinate a diverse range of plants. In the process of gathering food (pollen and nectar), bees transfer pollen from one flower to another, facilitating reproduction. I investigate two important aspects of foraging: pollination of an important crop by native bees and communication of floral resources by social bees.

Native bees that pollinate apples are an economically important and potentially limited resource. Native bees are often overlooked since orchard growers traditionally rely on managed honey bees for pollination. Given their potential to ameliorate the deficit of honey bee pollinators, it is important to identify the suite of apple pollinators in New York State, the life history of each native bee group in relation to apple pollination, and to promote their occurrence in and around apple orchards.

In order to facilitate visiting flowers, collecting nectar and pollen, and pollinating crops, honey bees have a language that conveys information from a recent foraging trip. This communication maximizes colony-level foraging efficiency and is achieved by a complex dance language. An interesting phenomenon in the dance language is the presence of distance-dependent error; precision increases as food-source distance increases. Here, I investigate three hypotheses for why there is imprecision within dances. Bees may be constrained, either physically or physiologically, to high precision for nearby food sources. Alternately, there may be an adaptive value to scattering recruits over a larger area.

Direction indicated within dances is gleaned from the sun's azimuth, but the extent to which the sun's position influences the precision of dances is unclear. Here, I test the hypothesis that error encoded in dances changes throughout the day.

Through a series of seminal experiments, Karl von Frisch decoded the honey bee's dance language. Since then, it has been widely accepted that there are two distinct types of dances: the round dance and the waggle dance and that they convey different information. Here I show that distance and direction information appears to be encoded in the same manner in both forms, suggesting that there is only one recruitment signal, the adjustable waggle dance.

BIOGRAPHICAL SKETCH

Kathryn Gardner grew up out side of Boston, MA and graduated high school from the Cambridge School of Weston in 1995. She attained her B.S. with honors in Biology from the University of Puget Sound in Tacoma, WA in 2001. Her undergraduate thesis was titled “Experimental analysis of worker division of labor in bumblebee nest thermoregulation (*Bombus huntii*, Hymenoptera: Apidae).” She worked under the guidance of Drs. Nick Calderone, Tom Seeley, Cole Gilbert, and Bryan Danforth for her Ph.D. in Entomology at Cornell University. Her dissertation combined a conservation-based analysis of native bee pollinators and a behavioral investigation of the dance language of the honey bee. After graduation, she plans on pursuing a career teaching biology.

For my grandparents

ACKNOWLEDGMENTS

I would like to thank the members of my committee, Nick Calderone, Bryan Danforth Cole Gilbert, and Tom Seeley for their help and support from the start. A special thanks goes to Tom, I would not be where I am today without your support and guidance. There were many people who helped me with the day to day research, G. Anderson, H. Chung, J. Drewes, J. Fox, M. Harro, B. Howell, A. Savage, F. Wen, A. Korol, B. Schiller, and M. Ryskin. My time in Ithaca has been great, mainly because of the close friendships that have developed over the years. Thanks to those who have stuck by me through thick and thin – you know who you are.

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CHAPTER 1

NOTES ON THE NATIVE BEE POLLINATORS IN NEW YORK APPLE ORCHARDS¹

1.1 Summary

I surveyed apple orchards in the Finger Lakes region of New York State. Pollinator guilds included honey bees and many native bee species known to be effective apple pollinators. Of the 31 native bee species collected, 14 species belong to eight subgenera of *Andrena*. Cavity-nesting mason bees were represented by a single female blue orchard bee, *Osmia lignaria* Say. The most numerous bees were mining bees in the genus *Andrena*. This chapter serves as a preliminary look at the native bee pollinators in apple orchards in New York State.

1.2 Introduction

New York State's apple industry ranks second nationally, with a crop worth over \$220 million in 2003 (USDA-NASS, 2006). Apple trees rely on cross-pollination for successful fruit set; thus, pollinating insects are economically valuable and a potentially limited resource. Traditionally, orchard growers rely on managed honey bee (*Apis mellifera* L.) colonies for pollination and often perceive them as the only important pollinators (see discussion in Parker et al., 1987). Honey bees are particularly valuable as pollinators of diverse crops in that they are pollen generalists (polylectic) and manipulation of population density is simple. However, this reliance on a single species is tenuous; any changes in honey bee populations can have a detrimental effect on the economy since it may affect crop quality and yield.

¹ This chapter is currently in press with slight modifications as Gardner, K.E. and Ascher, J.S. (2006) Journal of the New York Entomological Society. J.S.A. identified all bees and provided editorial comments.

Native bees have not received close study in the context of apple pollination, although they do visit apple blossoms and contribute to fruit set. Of the approximate 18,000 described bee species in the world, New York has more than 400 species that could potentially provide pollination services, but only some possess key characteristics that make them efficient and important apple pollinators. Important characteristics include pollen preference, size, abundance, and nesting habits as well as seasonality that coincides with apple bloom.

In light of the decline in honey bee populations in the past 50 years, it is important to identify the suite of apple pollinators in New York State and the life history of each native bee group in relation to apple pollination. I took 19 pollinator surveys from five orchards (Table 1.1) during apple bloom, from 4 May 2002 through 23 May 2002. Here I discuss which bee species are the prominent pollinators and how the life history characteristics determine the general effectiveness of native bees as apple pollinators.

The most numerous native bees were mining bees belonging to the genus *Andrena* (Andrenidae: Andreninae), which were collected in all orchards. Sweat bee females (Halictidae: Halictinae) and *Colletes inaequalis* (Colletidae: Colletinae) were also well represented at certain sites. Mason and leaf-cutter bees (Megachilidae: Megachilinae) were represented by a single female *Osmia lignaria* (blue orchard bee). Table 1.2 lists each bee species collected and their total abundance summed across all collections and orchards.

Table 1.1 Apple orchards in upstate New York where pollinator surveys were taken.

Orchard Site	Type of Orchard	Coordinates	County	Number of Collections	Commercial honey bees
A	Commercial	N42°26'42"W 76°27'50.4"	Tompkins	4	Yes
B	Commercial	N42°34'33.6" W76°34'58.8"	Tompkins	4	Yes
C	Private	N42°32'53.2" W76°39'0.7"	Tompkins	4	Yes
D	Small scale farm stand	N42°28'19.2" W76°32'52.8"	Tompkins	4	No
E	Private, abandoned	N43°4'44.4" W75°45'3.6"	Madison	3	No

Table 1.2 Index of pollinators in apple orchards with abundance (total number caught at 5 sites) and separated by sex. Other insects collected on apple blossoms included Coleoptera, Hymenoptera (e.g., Ichneumonidae), and Diptera (e.g., Syrphidae). All bees listed are native to New York except *Apis mellifera*.

Family				
Subfamily (common name)				
Genus (Subgenus) species	Author	Male	Female	Total
Andrenidae				
Andreninae (mining bees)				
<i>Andrena (Andrena) milwaukeensis</i>	Graenicher	1	0	1
<i>A. (Larandrena) miserabilis</i>	Cresson	0	6	6
<i>A. (Melandrena) carlini</i>	Cockerell	0	9	9
<i>A. (M.) dunningi</i>	Cockerell	0	18	18
<i>A. (M.) pruni</i>	Robertson	1	1	2
<i>A. (M.) regularis</i>	Malloch	1	21	22
<i>A. (M.) vicina</i>	Smith	0	6	6
<i>A. (Plastandrena) crataegi</i>	Robertson	19	2	21
<i>A. (Scrapteropsis) imitatrix</i>	Cresson	0	2	2
<i>A. (Simandrena) nasonii</i>	Robertson	4	1	5
<i>A. (Trachandrena) hippotes</i>	Robertson	1	1	2
<i>A. (T.) forbesii</i>	Robertson	0	7	7

Table 1.2 (Continued)

Family				
Subfamily (common name)				
Genus (Subgenus) species	Author	Male	Female	Total
<i>A. (T.) rugosa</i>	Robertson	0	3	3
<i>A. (Tylandrena) perplexa</i>	Smith	2	2	4
Apidae				
Apinae (includes eusocial corbiculate bees)				
<i>Apis mellifera</i>	L.	0	205	205
<i>Bombus (Psithyrus) citrinus</i>	Smith	0	1	1
<i>B. (Pyrobombus) impatiens</i>	Cresson	0	2	2
<i>B. (P.) perplexus</i>	Cresson	0	1	1
Xylocopinae (small and large carpenter bees)				
<i>Ceratina (Zadontomerus) calcarata</i>	Robertson	2	0	2
<i>Xylocopa (Xylocopoides) virginica</i>	L.	3	3	6
Colletidae				
Colletinae (cellophane bees)				
<i>Colletes inaequalis</i>	Say	0	10	10
Halictidae				
Halictinae (sweat bees)				
<i>Agapostemon (Agapostemon) sericeus</i>	(Forster)	0	1	1
<i>Augochlorella aurata</i>	(Smith)*	0	2	2
<i>Halictus (Seladonia) confusus</i>	Smith	0	1	1

Table 1.2 (Continued)

Family				
Subfamily (common name)				
Genus (Subgenus) species	Author	Male	Female	Total
<i>Lasioglossum (Dialictus) cressonii</i>	(Robertson)	0	1	1
<i>L. (D.) cf. admirandum</i>	(Sandhouse)	0	6	6
<i>L. (D.) foxii</i>	(Robertson) [formerly in <i>Evylaeus</i>]	0	4	4
<i>L. (D.) imitatum</i>	(Smith)	0	5	5
<i>L. (D.) versans</i>	(Lovell)	0	2	2
<i>L. (D.) metallic</i>	spp.	0	2	2
<i>L. (Evylaeus) cinctipes</i>	(Provancher)	0	1	1
Megachilidae				
Megachilinae (mason bees)				
<i>Osmia (Osmia) lignaria</i>	Say	0	1	1

*=*Augochlorella striata* (Provancher) (synonymy: Coelho, 2004)

1.3 Discussion

1.3.1 Honey bees

The honey bee (*Apis mellifera*) was the most abundant species in all but one site (Site E), including a site that does not use commercial honey bees (Site D). The average number of honey bees caught per collection at orchards that used managed honey bees (mean \pm SE; 14.8 ± 3.8 ; $n = 12$) was slightly higher compared to those orchards that did not use managed honey bees (6.4 ± 2.0 ; $n = 7$), although this difference was not significant at the 0.05 level ($t_{15} = -1.96$, $P = 0.069$). This may be an example of un-managed feral honey bees providing pollination services (Chang and Hoopingarner, 1991). Alternatively, honey bees may be foraging from distant managed colonies, leading to ‘spillover’ pollination (Morse and Calderone, 2000).

In the following analyses, I use relative proportion of honey bees per collection and absolute number of native bees per collection to avoid collinearity. Temperature (data collected retrospectively from WeatherUnderground, 2006) had a significant effect on the proportion of honey bees collected; more honey bees were collected as temperatures increased ($F_{1, 18} = 6.15$, $P = 0.023$). The proportion of honey bees among all bees collected increased when the mean daily temperature was above 13°C (after Vicens and Bosch, 2000a); the mean proportion of *Apis* on days below 13°C was $32.7 \pm 8\%$ ($n = 7$) while the mean proportion on days above 13°C was $64.9 \pm 6\%$ ($n = 12$; $t_{12} = -2.80$, $P = 0.016$). Honey bees are relatively less numerous than native bee pollinators at lower temperatures, but become the most numerous pollinators as temperature increases (Boyle-Makowski, 1987). Additionally, the number of native bees did not differ between days above 13°C and days below 13°C ($t_{12} = 1.69$, $P = 0.117$), indicating that they consistently forage through all temperatures above their flight threshold.

1.3.2 Mining bees

Several species of *Andrena* subgenus *Melandrena* possess many characteristics that make them particularly valuable apple pollinators: 1. Season of flight (phenology): they emerge very early in spring (the last week of March in central New York in warm years) and mate and begin nest construction well before apple bloom, so females are actively collecting pollen at the onset of apple bloom. 2. Pollen preference: they exhibit a preference for apple bloom. 3. Size: they are relatively large, facilitating the collection and transfer of pollen. 4. Abundance: they nest gregariously in very large numbers, often digging burrows in sandy, open ground within orchards (Schrader and LaBerge, 1978). *Andrena carlini*, *A. dunningi*, *A. regularis*, and *A. vicina* are among the most widely distributed and numerous *Andrena* (*Melandrena*) species across New York State, New England, and southeastern Canada, and were collectively found in high abundance in my surveys.

The gregarious (and sometimes communally nesting) *A. (Plastandrena) crataegi* was well represented in my samples. However, my specimens were mostly males (19 of 22), which are typically more conspicuous than females early in the flight season because of the protandrous mating system (Osgood, 1989). Due to the relatively late period of flight of this species, peak pollen collecting activity by *A. crataegi* females may occur later than peak apple bloom, reducing the value of this species as an apple pollinator.

1.3.3 Bumble bees

The most common bumble bee species in my samples were *Bombus (Pyrobombus) impatiens* and *B. (P.) perplexus*. Although not numerous during apple bloom, bumble bees are proficient pollinators because of their large size, dense hair, and temporary loyalty to rewarding floral resources such as apple blossoms (Heinrich,

1976; Heinrich, 1979). Another species collected, *B. (Psithyrus) citrinus*, is a social parasite of other bumble bees that does not actively collect pollen but nonetheless may aid in transferring pollen during nectar collection due to its large size and dense hair.

Bumble bees are exceptionally valuable pollinators on an individual basis (Jacob-Remacle, 1989) but are not present in high numbers during apple bloom. Boyle and Philogène (1983) and Boyle-Makowski (1987) attribute the low numbers to resource competition with honey bees. Although indirect competition for floral resources may plausibly reduce native populations, most critical studies to date failed to find decisive evidence that the presence of honey bees has a population-level impact on native bee species (Steffan-Dewenter and Tschardtke, 2000; Roubik and Wolda, 2001); although Goulson (2003) points out that this is not a conclusive finding. An alternative explanation considers that seasonal abundance of *Bombus* spp. is dictated by the social structure and timing of colony foundation. During apple bloom, *Bombus* exist in a solitary phase and are therefore scarce; queens (the only caste present) are either searching for nesting sites or provisioning the first brood. Bumble bees become far more numerous after apple bloom as the number of workers increases.

1.3.4 Sweat Bees

Halictids were abundant at one collection site (site E). According to Boyle-Makowski (1987), sweat bees can be effective apple pollinators, and are often more efficient than honey bees since they carry more fruit pollen (as opposed to flower pollen) and their abundance does not deviate with changing temperatures. However, in my surveys, most halictids were species of *Lasioglossum*, subgenus *Dialictus*, not mentioned by Boyle-Makowski (1987). These small halictines are generally abundant but may be relatively less important apple pollinators because of a generalized pollen preference, small size, and relatively short, sparse hair.

1.3.5 Mason bees

One *Osmia lignaria* (blue orchard bee) female was the only megachilid bee found in my samples. Species of *Osmia* (*Osmia*), including the native *O. lignaria* and the deliberately introduced *O. cornifrons*, are particularly effective apple pollinators (Torchio, 1976; Batra, 1998), but may be too scarce to contribute much as unmanaged apple pollinators in central New York. Mason bees nest in hollow cavities in older wood, which may be scarce in and around managed orchards where trees are regularly pruned.

1.3.6 Cellophane bees

Colletes inaequalis is a large ground-nesting bee that visits a wide range of trees and shrubs, including apples. It is the earliest native bee to emerge in central New York, and is present in high numbers during apple bloom, but is primarily associated with *Acer* (maple; Batra, 1980). *Colletes* typically nest in large aggregations (Batra, 1980) that may provide valuable pollination services since aggregations persist over many years and can contain thousands of bees. Although they were well represented in my study, collected in three of the five orchards, a tight association with particular nesting substrates may limit the general occurrence of *C. inaequalis* in orchards.

1.4 Conclusion

There is a variety of native pollinators present in apple orchards in New York; however, the mere presence of a species does not indicate that it plays an important role in pollinating apples. The most numerous native pollinators in apple orchards are in the family Andrenidae, the subfamily Andreninae, and the genus *Andrena*. The subgenera *Melandrena* and *Trachandrena* are particularly important, being found in

high numbers and gathering pollen during apple bloom. It is important to maintain a natural habitat that is suitable for *Andrena* and other native pollinators, ensuring that these important native bees are present in an apple orchard and will contribute to fruit set. Specifically, adequate nesting sites must be available; the majority of ground nesting bees prefer semi-bare or sparsely vegetated soil. Providing alternative forage plants before and after apple bloom as well as removing competing bloom encourages native bees to visit apple flowers.

In order to get a complete picture of the suite of apple pollinators a multi-year study is necessary since bee populations fluctuate annually in response to weather or other environmental factors. Therefore, this chapter is meant to be an impetus for additional research into the key native pollinators of apples in New York State.

CHAPTER 2

A REVIEW OF NATIVE BEE POLLINATORS IN APPLE ORCHARDS OF NEW YORK: RELATIVE IMPORTANCE AND MANAGEMENT STATUS²

2.1 Summary

Honey bee populations across North America have declined over the past 50 years. There is evidence that suggests that native bee populations are also declining, making it important to define and characterize native bees and the roles they play as crop pollinators. The relative importance of the native bee groups as unmanaged pollinators and their potential for management is related to aspects of their natural history. To increase pollination by native bees, I suggest that greater effort be made to conserve and enhance existing populations of native bee species, particularly large-bodied, early emerging, and gregarious species of *Andrena* (including species of subgenera *Melandrena* and *Trachandrena*), through inexpensive soil and ground cover manipulation in and around orchards, rather than introducing or promoting exotic species as pollinators. Recently identified threats to native bee orchard pollinators posed by exotic parasites associated with managed bees are briefly reviewed.

2.2 Introduction

Both feral and managed honey bee populations have declined in the past 50 years due to parasites, disease, the threat of Africanized honey bees, and a reduced profit margin for beekeepers because of imported honey (Watanabe, 1994; Allen-Wardell et al., 1998; Degrandi-Hoffman, 2003). Additionally, numbers of individuals

² This paper is currently in press with slight modifications as Gardner, K.E. and Ascher, J.S. (2006) Journal of the New York Entomological Society. J.S.A. provided significant editorial comments.

and species of native bees in areas with intensive agriculture may be low (Buchmann and Nabhan, 1996; Kremen et al., 2002) although determining if a population decline is serious is difficult (Roubik, 2001). Therefore, it is important to identify the suite of apple pollinators in New York State, characterize the relative value of each group, and develop appropriate conservation and management schemes for native orchard pollinators. This chapter aims to increase the awareness of ‘free’ pollination provided by native bees in the Finger Lakes area of central New York and to propose simple, inexpensive steps that could increase the pollination services provided by native bees.

Approximately 18,000 bee species are described worldwide, 3,500 species are native to America north of Mexico, and more than 400 are native to New York State, of which over 300 species are native to the Finger Lakes Region. Many native bee species could potentially provide pollination services; however not all species are equivalent. Five life history characteristics are key when considering the importance of a bee species or group as a pollinator for a given crop (see also Batra, 1997): phenology, pollen preference, abundance, pollinating efficacy (see Thomson and Goodell, 2001), and nesting habits, including site choice and sociality. The interaction of these five characteristics is essential when considering the significance and potential for management of native bee groups (Gardner and Ascher, 2006).

This chapter reviews the suite of pollinators in New York apple orchards and examines how life history characteristics influence the relative effectiveness as apple pollinators and the prospects for improving the conservation and management of non-*Apis* orchard pollinators. Although I focus on apple orchards in New York, analyses of surveys interpreted using knowledge of pollinator life history can be applied to any agricultural crop that utilizes insect pollinators. I present a review of the major bee groups known to pollinate apples, mining bees, bumble bees, cellophane bees, and mason bees; a discussion about the impact of exotic bees on native bees follows.

2.3 Discussion

2.3.1 *Andrena* mining bees

The genus *Andrena*, consisting of small to moderately sized, soil-nesting, mining bees, is the most species-rich bee genus in temperate North America and Europe with about 1,450 species, and includes many numerous, widely distributed, and efficient apple pollinators (Brittain, 1933; Johnson, 1984; Boyle-Makowski, 1987; Jacob-Remacle, 1989). *Andrena* species transfer pollen efficiently because they possess relatively dense pubescence, including specialized tibial, femoral, trochanteral, and propodeal pollen-transporting scopal hairs. Many of the 87 *Andrena* species known from New York State visit apples, but certain early emerging species of subgenera *Melandrena* (10 species in New York State) and *Trachandrena* (12 species in New York State) are likely to be the most important orchard pollinators. The most numerous *Andrena* (*Melandrena*) species across New York State, New England, and southeastern Canada are *A. carlini* Cockerell, *A. dunningi* Cockerell, *A. vicina* Smith, and *A. regularis* Malloch (an important pollinator of blueberries but not a *Vaccinium* specialist, contra Sheffield et al. (2003), see Bouseman and LaBerge (1979)).

Subgenus *Andrena* s.str. includes several moderately sized, early emerging species, such as *A. milwaukeensis* Graenicher, *A. mandibularis* Robertson, and *A. rufosignata* Cockerell, which commonly collect pollen from rosaceous trees (LaBerge, 1980). Although often seen visiting apples and other fruit trees in New York, these bees seem scarce in large orchards, perhaps reflecting less gregarious nesting habits and a preference for more natural woodland habitats.

Males of another widely distributed and generally numerous, early emerging bee, *Andrena* (*Larandrena*) *miserabilis*, have been observed swarming about apple trees on the Cornell University campus. *A. miserabilis* is “a very common, widespread spring bee and surely plays a very important part in the pollination of fruit

crops” (Ribble, 1967, p. 37). However, females of this species may be less effective pollinators than those of *Melandrena* and *Trachandrena* species due to their smaller body size (female length about 7-8 mm versus about 10-14 mm for common *Melandrena* species, about 10-11 mm for common *Andrena* s.str. species, and about 8-10 mm for common *Trachandrena* species; measurements from Mitchell, 1960).

Other *Andrena* species with no specific association with apples are numerous in orchards. The species *Andrena (Simandrena) nasonii* Robertson is very widely distributed and numerous across eastern North America and is a potentially important pollinator of many crops across the region (see LaBerge, 1980 for host records) due to its highly polylectic nature.

Species of *Andrena*, specifically species of subgenera *Trachandrena* and *Melandrena*, are ideal candidates for management in apple orchards. They are native species, present in high numbers during apple bloom, show a preference for apple flowers, and often nest in large aggregations. Additionally, these *Andrena* are individually better pollinators than *Apis mellifera* L., they carry more fruit pollen and their numbers do not appreciably fluctuate with changing weather conditions, as honey bees do (Boyle and Philogène, 1983; Boyle-Makowski, 1987). Currently, these bees are not managed, although attempts have been made (see Butler, 1965).

2.3.2 Bumble bees

Early emerging, cold tolerant species of the closely related subgenera *Pyrobombus* and *Bombus* s.str. (Kawakita et al., 2004) are the most numerous bumble bees present in orchards, followed by later-emerging species of subgenus *Fervidobombus*. Bumble bees are relatively scarce during apple bloom, most likely due to the timing of colony founding; bumble bee workers become numerous well after apple bloom. However, bumble bee queens are proficient pollinators because of

their large size, dense hair, and temporary loyalty to rewarding floral resources such as apple blossoms (Heinrich, 1976; Heinrich, 1979).

Bumble bees, usually the native *Bombus impatiens* Cresson in the eastern United States, are commercially available year-round. A single hive can contain several hundred individuals that forage at cooler temperatures, visit more flowers per minute, and carry more fruit pollen than honey bees (Javorek et al., 2002). These bees are typically used for greenhouse pollination of tomato and blueberry crops requiring buzz pollination. Since they are commercially reared and available year round, bumble bees are available for apple pollination, but may be too costly to provide a practical solution. Encouraging queens to start nests in the area is beneficial and easy to do (Barron et al., 2000), although bumble bees cannot be relied upon as the sole pollinators due to insufficient numbers during apple bloom. Nesting domiciles placed in and around an orchard are attractive to queens searching for nest sites and encourage them to nest. Although no workers are present during apple bloom, queens are proficient pollinators and undoubtedly contribute to fruit set.

There is evidence of a troubling decline in North American *Bombus* s.str. species. Two locally occurring species of *Bombus* s.str., *B. affinis* Cresson and *B. terricola* Kirby, which should be important apple pollinators in New York State, were not collected in a recent survey (Gardner and Ascher, 2006) and have been generally absent (*B. affinis*) or unusually scarce (*B. terricola*) in the Ithaca, NY, vicinity since 1999. Another species of subgenus *Bombus* closely related to and perhaps conspecific with *B. terricola*, *B. occidentalis* Greene, has disappeared from the San Francisco Bay area of California and elsewhere in western North America since about 1995. In New York State, declines of *Bombus* s.str. seem to be general. Declines in four *Bombus* s.str. species in both eastern and western North America occurred concurrently with development and spread of *B. occidentalis* and *B. impatiens* as greenhouse pollinators.

The cause of declines in native North American *Bombus* s.str. species has not been proven (see Goulson et al., 2005; Williams, 2005), but the culprit is suspected to be *Nosema* parasites transferred to *B. occidentalis* from a non-native *Bombus* s.str. species, the European *B. terrestris* L., when these two closely related species were housed together during greenhouse trials (also see Niwa et al., 2004).

2.3.3 Sweat Bees

Halictidae are small to medium sized bees that are often metallic in color. Most halictids nest in the ground and can form large nesting aggregations. While halictids are present in orchards (Boyle-Makowski, 1987; Gardner and Ascher, 2006) and may contribute to fruit set, they are probably not as effective pollinators as *Andrena*, *Osmia*, or *Bombus* due to their generalized pollen preferences and relatively short, sparse hair, and to the small size of the most common species.

2.3.4 Cellophane bees: *Colletes*

Colletes nest in large aggregations that may provide valuable pollination services since aggregations persist over many years and can contain thousands of bees. In central New York, *Colletes inaequalis* Say is the first native bee to emerge in the spring, and is still present in large numbers during apple bloom; however, its tight association with a particular nesting substrate and its affinity for maple (*Acer*; Batra, 1980) may limit its general presence in apple orchards and therefore its effectiveness as an apple pollinator.

Ground nesting bees prefer soil that has low organic carbon content and a loose or pliable O-horizon (Osgood, 1972). Orchard growers can encourage soil-nesting *Colletes*, *Andrena*, and halictine bees to nest in the area or enhance existing populations by manipulating these soil characteristics to provide an attractive nesting

site. It may also prove feasible to induce aggregations by applying synthetic mandibular gland pheromones, a known attractant to soil-nesting bees (Batra, 1978). Both male and female *Colletes* spp. respond to a synthetic blend of mandibular gland secretions, which, in nature, may serve to create and maintain nesting aggregations (Batra, 1980). Theoretically, a one-time application of appropriate chemicals to an area where bees are desired may induce these bees to form a permanent nesting aggregation. Once established, nesting aggregations are resilient, can grow to large sizes, and typically include many species. Artificial nest aggregations of *Colletes* spp. have been successfully started in Maryland (Batra, 1980). Once nests are complete, they can be transferred to new nest sites near crops that require pollination (Torchio, 1991). Care should be taken to protect established nest sites: they should be minimally disturbed, not tilled or paved, and not re-vegetated since bare or sparsely-vegetated soils are preferred.

2.3.5 Mason bees

Species of *Osmia* s.str., including *O. lignaria* Say, are particularly effective pollinators of apple (Torchio, 1976; Batra, 1998). The European species *O. cornuta* Latreille has been shown to be more effective at pollinating apples than *A. mellifera* because of a higher rate of contact with the stigma (Vicens and Bosch, 2000b). However, mason bees may be too scarce to contribute much as unmanaged apple pollinators in central New York (Gardner and Ascher, 2006). Mason bees nest in hollow cavities in older wood, types of nest sites that may be scarce in and around managed orchards where trees are pruned.

Megachilidae (*Osmia* spp.) are important pollinators of blueberry and cranberry, *Vaccinium* spp., in Maine, New Jersey, and Nova Scotia. *Osmia* spp. are proficient apple pollinators as well, though they are not always present in high

numbers. However, increasing local populations is relatively easy and would enhance fruit set and fruit quality within an apple orchard. There are two ways to increase the local abundance of these bees: 1) providing nesting sites and 2) planting certain forage plants around the orchard. *O. lignaria* nest in cavities in wood, such as raspberry and blackberry canes, sumac, and in the holes made by other insects in dead trees and wooden fences. These nesting sites are limited and may restrict local populations, especially in managed apple orchards. However, inexpensive artificial nests (either wood blocks with holes of a specific size and depth or cardboard straws) can be purchased or constructed that will attract these bees to the area (see www.osmia.com). Once present, the bees will reuse the same nesting hole for several years. Planting and maintaining alternate forage around apple orchards will also encourage these bees to come to the area. Plants, such as willow (*Salix* spp.), cherry (*Prunus* spp.) and honeysuckle (*Lonicera* spp.), provide an attractive source of pollen and nectar before and after apple bloom. Immature stages of these bees can be purchased and placed in an orchard at the appropriate time so that emergence coincides with the bloom period (Bosch and Kemp, 2000).

Recently, *Osmia (Osmia) cornifrons* Radoszkowski has received considerable attention as a potential commercial apple pollinator in the USA (Batra, 1998). This species now occurs in the Ithaca, NY area and is widespread in southern New York. *Osmia cornifrons* is a proficient pollinator of apples and has been managed for apple pollination in Japan for over 60 years. Introduced deliberately by the USDA for apple pollination, populations of *O. cornifrons* are now found away from orchards in several localities in New York State including Tompkins, Orange, Putnam, Rockland, and New York (including Central Park, Manhattan) counties (J.S. Ascher, personal communication). Discovery of *O. cornifrons* populations far removed from orchards is not surprising, since it was known prior to its release to be polylectic rather than an

apple specialist. This species is so similar in behavior and morphology to the native *O. lignaria* that competitive and other interactions between these species seem inevitable (see Goulson, 2003; Goulson, 2004). Indeed, a male *O. cornifrons* collected in Central Park, New York on 10 April 2004 was grasping a female *O. lignaria*, apparently in copula (J.S. Ascher, personal communication).

2.4 Conclusion

Honey bees are heavily relied upon for crop pollination needs in the United States. However, disease, parasites, and pesticides have contributed to the decrease of honey bee populations, both managed and unmanaged. Therefore, it is prudent to investigate additional or alternative sources of crop pollination. This information will also document fluctuations within pollinator populations, which may serve as an important indicator of environmental health (Kevan, 1999). A variety of native pollinators are present in New York apple orchards, but the mere presence of a species does not ensure that it plays an important role in pollinating apples. Based on five characteristics: phenology, pollen preference, abundance, pollination efficacy, and nesting habits, I believe the most valuable native bee pollinators in apple orchards may be moderate to large species belonging to the genus *Andrena*, especially early emerging species of subgenera *Melandrena* and *Trachandrena*. However, many bees (e.g., *Bombus*, Halictidae, *Colletes*) are present in apple orchards and contribute to fruit set. Indeed, diversity is important when considering crop pollination (Westerkamp and Gottsberger, 2000).

Exotic bees may harm native species through competition for floral resources, competition for nest sites, introduction of parasites and pathogens, altering the seed set of native plants, pollination of weeds (Goulson, 2003), and mating interference. These threats are not merely hypothetical. The torymid *Monodontomerus osmiae* Kamijo, an

ectoparasitoid of Japanese *Osmia* s.str. including *Osmia cornifrons*, has been reared from nests of purportedly native *Osmia* species in Silver Springs, Maryland (Grissell, 2003). This is near the site of introductions of *O. cornifrons* from Japan by USDA scientists at Beltsville, Maryland. Furthermore, an additional *Osmia* s.str. species closely resembling *O. cornifrons*, *Osmia (Osmia) taurus* Smith (also a host of *M. osmiae*), has been field-collected in the USA around Beltsville, Maryland (Cane, 2003) and in southern Pennsylvania. The most logical source of a recent introduction of these Japanese species to Maryland is as stowaways in shipments (from Japan to USDA scientists) putatively containing only parasite-free *O. cornifrons*. Given that the effects of non-native bees are not fully understood (Paini, 2004), I recommend that efforts to manage bees focus on honey bees, well established exotic bees such as *M. rotundata* F., and native species, such as *Andrena* spp., and that additional deliberate introductions be prohibited.

A new concern facing native bees has been raised recently – the impact of the non-native honey bees on native bee populations. While it is beyond the scope of this chapter to go into depth, this subject warrants mention. Non-native species have long been known to harm populations of native species through competitive exclusion, but we seem to disregard bees (Goulson, 2004). There is no conclusive evidence about the impact of the presence of *Apis mellifera* on native bee species, because the relationship is complex (Kato et al., 1999; Steffan-Dewenter and Tscharntke, 2000; Roubik and Wolda, 2001; Thomson, 2004; Forup and Memmott, 2005; Moritz et al., 2005; Paini and Roberts, 2005).

In general, it is important to maintain suitable nesting habitats for native bees to ensure that large populations of these important pollinators are present in an apple orchard and will contribute to fruit set. Adequate nesting sites, either natural or artificial, must be available, such as semi-bare or sparsely vegetated soil. Orchard

management usually entails meticulous grooming of the ground, often reducing any potential nesting sites. Therefore, it is beneficial to leave some ground unmanaged, possibly around the perimeter of the orchard (see also Russell et al., 2005). Another common orchard management practice is to remove competing bloom to force bees (usually thought of only in reference to honey bees) to visit only the apple flowers. This also is effective in enticing the native bees to restrict their visits to apple blossoms, since *Andrena* spp. and *Bombus* spp. commonly visit many other flowers (Kendall and Solomon, 1973) such as dandelions (*Taraxacum officinale*); maintaining alternative forage before and after apple bloom will also encourage native bees to remain in the area long-term. The use of pesticides is also problematic. Depending on the timing of application and the specific chemical being applied, bees may be adversely harmed (Thompson, 2001; Gels et al., 2002). Pesticide or fungicide applications should be timed to reduce contact with foraging bees, such as late in the evening. In addition, application of chemicals should be minimized in areas where native bees are nesting.

CHAPTER 3

DIRECTIONAL IMPRECISION IN THE HONEY BEE'S WAGGLE DANCE: CONSIDERING ADAPTIVE AND NON-ADAPTIVE HYPOTHESES³

3.1 Summary

Honey bees use a complex dance behavior that encodes the distance and direction to profitable food sources, but these dances do not contain precise directional information for nearby (<700 m) food sources. The reason for this imprecision has been the subject of recent debate. Some have suggested that imprecision within dances is non-adaptive, i.e., that dancing bees are limited in their ability to indicate more precise directional information; we examine two hypotheses regarding possible limitations. The 'brief-return-phase' hypothesis proposes that when signaling a nearby food source, the duration of the return phase (the time between successive waggle phases) is brief and a dancing bee does not have enough time or space to orient her waggle phases precisely. Similarly, the 'brief-waggle-phase' hypothesis proposes that a short waggle phase duration prevents dancing bees from precisely orienting their waggle phases. Other investigators have suggested that the imprecision within dances is adaptive. The 'tuned-error' hypothesis proposes that the imprecision in dances serves to spread recruits over an optimal patch size tuned by natural selection. Here I investigate these three hypotheses by analyzing 572 dances for food sources at 10 distances from the hive. I found that the duration of the return phase does not differ in dances for near and far food sources, indicating that the imprecision is not caused by limitations imposed by brief return phases. I also found that the scatter of waggle

³ This chapter is currently in press with slight modifications as Gardner, K.E., Seeley, T.D., and Calderone, N.W. (2006). *Entomologia Generalis*. T.D.S. and N.W.C. provided significant contributions and editorial comments; N.W.C. provided financial support and statistical assistance.

phase angles after left or right turns does not steadily increase as waggle phase duration decreases, indicating that the imprecision is not caused limitations imposed by brief waggle phases. Finally, I found that while the patch size indicated within dances increases as distance to the food source increases, it does so at a rate significantly less than would be expected if the bees were not adjusting their directional information in response to distance, supporting the hypothesis of an adaptive value to the imprecision within dances for nearby food sources.

3.2 Introduction

Upon returning from a profitable foraging trip, a bee performs a dance that encodes the approximate distance and direction of the food source (von Frisch 1993). These dances have a stereotypical form consisting of a series of alternating waggle and return phases (Figure 3.1a). During a waggle phase, the bee orients her body in a given angle relative to gravity and shakes her body from side-to-side. She then turns left or right and walks back in a semi-circle to her approximate starting position; this is the return phase. Distance to the food source is encoded in the duration of the waggle phase in which longer waggle phases indicate farther food sources. Direction to the food source is encoded in the angular orientation of the waggle phase. The angle of the food source with respect to the sun corresponds to the angle of the waggle phase with respect to gravity. Dances for food sources less than 100 m away do not follow the typical form, instead, bees run in circles, alternating left and right turns, sometimes with a waggle phase, sometimes without. Von Frisch (1974) called these less regularly formed dances ‘round’ dances, which are typically thought to lack directional information, however, more recent studies have shown otherwise (chapter 5; Kirchner et al., 1988; Jensen et al., 1997).

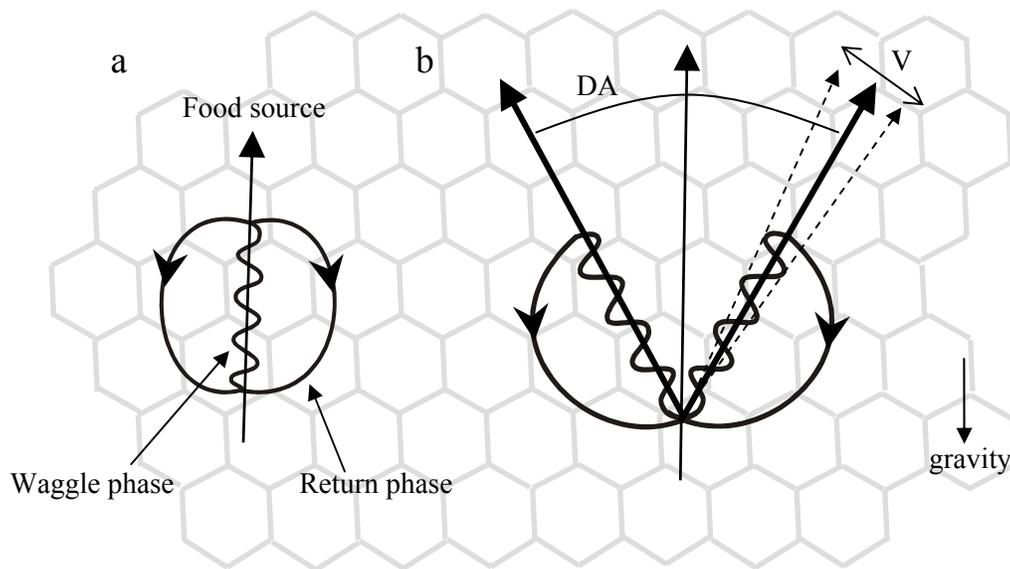


Figure 3.1 a and b Dance form and imprecision in the waggles dance of the honey bee. 3.1a: stereotypical depiction of the waggles dance showing the return and waggle phases. 3.1b: Actual form of waggles dance for nearby dances (less than 700 m). Notice that a waggle phase that follows a left turn deviates to the right of the expected angle and vice versa. In this instance, the dancer would be indicating a food source in the direction of the sun. The two types of imprecision shown are (1) divergence angle (DA): the difference between the mean bearings of left and right waggle phases and, (2) variance (V): the scatter of angles of left or right waggle phases.

The waggle phase contains the most information in the dance, but the information is not presented precisely for nearby (<700 m) food sources. Sequential waggle phases deviate in bearing from each other giving rise to a bimodal distribution of waggle phase bearings. This spread is known as the divergence angle (Figure 3.1b), and I define it as the difference between the mean angles of waggle phases, with respect to gravity, following left or right turns (hereafter called left or right waggle phases). Another source of imprecision is the variance within left or right waggle phases (figure 3.1b). Although each waggle phase contains information about the location of a point in space (i.e., distance and direction from the hive), a dancer does not consistently indicate the same information throughout her dance. Given that each dance can contain up to 200 waggle phases (Seeley, 1995) and that a follower bee typically follows approximately 10 waggle phases (Esch and Bastian, 1970; Judd, 1995), the information received by different follower bees may vary widely.

The evolutionary basis of the imprecision within dances for nearby food sources is a puzzle. This imprecision may be non-adaptive (the result of limitations on the bees' abilities to orient their dances) or it may be adaptive. If the imprecision arises from a constraint, then it may be that the brevity of the return phase or of the waggle phase in dances for nearby food sources imposes a limit on the bee's ability to orient the waggle phases. Beekman et al. (2005) investigated the former possibility in dances for food sources 100-250 m from the hive by placing feeders at different distances in a tunnel, which exaggerates a bee's perception of the distance she has flown (see Srinivasan et al., 2000). According to their data, the bees ability to dance precisely is physically constrained because the return phase duration was smaller when the advertised site was nearby compared to when it was distant. If the relationship between return phase duration and food-source distance is positive, then it follows that return phases for nearby food sources must be completed rapidly. Beekman et al.

(2005) argue that as the return phase gets shorter, the dancing bee has less time or space to realign her body in the appropriate angular orientation for successive waggle phases. I call this the brief-return-phase hypothesis, see Table 3.1. A critical prediction of this hypothesis is that as the distance to a food source increases, there is a steady increase in the return phase duration.

Another possibility is that the bees are constrained by brief waggle phases. It is well known that waggle phase duration changes in accordance with distance to the food source (von Frisch, 1993). Dances for nearby food sources have brief waggle phases which may impose a physiological limit to precision; the dancers may not be capable of precisely orienting waggle phases when they are extremely brief. Orientation to gravity on the comb in the dark hive is directed by proprioceptors on the body of the bee (Horn, 1975; von Frisch, 1993; Dyer, 2002). It may be that the duration of a given waggle phase modulates the computation of subsequent waggle phases based on information provided by the bee's gravity receptors. As waggle phase duration increases, the information that the bee receives from its gravity receptors may be more consistent, such that subsequent waggle phases are more precise. I call this the brief-waggle-phase hypothesis, see Table 3.1. A critical prediction of this hypothesis is that as the distance to a food source increases, there will be a steady decrease in the variance of the angles of the left or right waggle phases, indicating that bees are able to orient their waggle phases with increasing precision as the duration increases.

An alternative possibility is that directional imprecision within dances is beneficial to the colony. Haldane and Spurway (1954) and Wilson (1962) suggest that imprecision in recruitment signals could be adaptive. This hypothesis was later formalized by Towne and Gould (1988) as the 'tuned error' hypothesis, which states that directional imprecision within dances serves to spread recruits over an optimal

Table 3.1 Three hypotheses for why there is directional imprecision in waggle dances for nearby food sources

Hypothesis	Summary	Critical Prediction
Constraint hypothesis 1: Brief-return-phase hypothesis	Dances for nearby food sources have brief return phases, which prevent bees from precisely orienting their waggle phases.	As the distance to a food source increases, there will be a steady increase in the duration of the return phase, which enables bees to orient their waggle phases more precisely.
Constraint hypothesis 2: Brief-waggle-phase hypothesis	Dances for nearby food sources have brief waggle phases, which prevent bees from precisely orienting their waggle phases.	As the distance to a food source increases and thus waggle phase duration increases, there will be a steady decrease in the variance of the bearings of waggle phases after left or right turns. Also, the variance decreases as long as the divergence angle decreases. This indicates that bees are able to orient their waggle phases more precisely as distance increases.
Adaptation hypothesis: Tuned-error hypothesis	Dances for nearby food sources have a bimodal distribution of waggle phase bearings, to help spread recruits across a flower patch.	As the distance to a food source increases, there will be a decrease in the divergence angle, which will stabilize the size of the area over which recruits are dispatched.

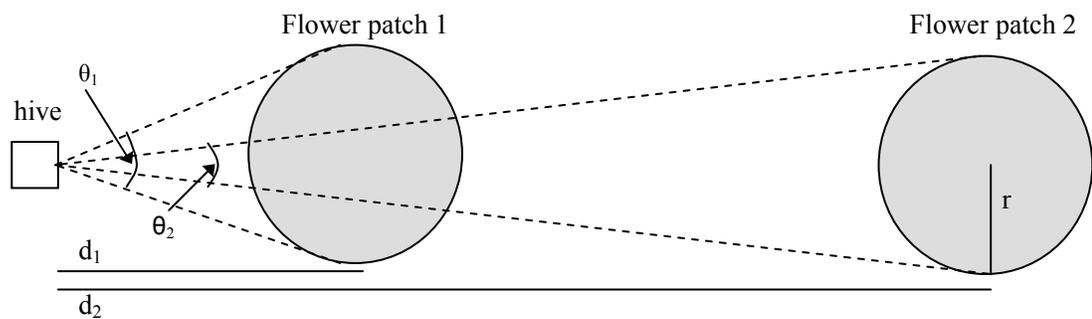


Figure 3.2 Divergence angles needed to maintain a constant patch size across distances. Divergence angles (θ_1 and θ_2) must decrease as distance to a flower patch increases to maintain constant patch size. An assumption shown here is that direction and distance scatter are similar, so the approximate area to which dancer bees are sending recruits to is circular, as opposed to oval if the distance or direction scatter were different from each other. Figure after Towne and Gould (1988).

area, and this area remains constant regardless of the distance of the food source from the hive (Figure 3.2). The patch size can be calculated from parameters within individual dances. If a ‘patch’ is considered as a circular area, the directional scatter is encoded in the divergence angle and the distance scatter is encoded in the variation in the waggle phase duration. When looking at the scatter of recruits, Towne and Gould (1988) found that it increases slightly as distance to the food source increases; they conclude that the scatter of recruits has been tuned by natural selection to allow a colony to exploit potential food sources with greater efficiency, even though their data do not exactly match the prediction of the hypothesis. Their study investigated the behavior of recruits outside the hive; I look at what is happening inside the hive and examine the behavior of dancing bees to see the messages that they are sending to the recruits. A critical prediction of the tuned-error hypothesis is that I will see a relatively constant patch area indicated within the dances regardless of distance to the food. Here I test three hypotheses (Table 3.1) by recording and analyzing 572 dances for food sources at 10 distances from the hive.

3.3 Methods

3.3.1 Observation Hives, Artificial Feeders, and Recording Dances

I recorded dances from three unrelated colonies (A, B, and C); A and C were housed in two-frame observation hives while B was housed in a four-frame observation hive. Colony size does not appear to influence dance behavior (Beekman et al., 2004). The specifications of the observation hives are described elsewhere (Seeley, 1995, ch. 4). To facilitate observations, I confined dances to a specific area of the comb by fitting each hive with a wedge that forced bees to enter on one side (Visscher and Seeley, 1982). Colonies were housed at two locations (A and C were together), within Ithaca, NY, USA W76° 29', N42° 26'.

The bees were trained to an artificial feeder of 0.5 to 2.0 M sucrose solution scented with anise oil (60 μ l/l) using the methods of von Frisch (1993, p. 17). Sucrose concentration was varied and new recruits were captured to reduce crowding at the feeder, which can inhibit dancing upon returning to the nest (Fernández and Farina, 2002; Thom, 2003). Foragers were individually marked with paint (mixture of clear shellac and dry artist's pigment) and their dances were recorded upon their return to the hive.

Dances performed by marked bees were videotaped at 30 frames per second using a Sony mini-DV camcorder (DCR-TRV50). The feeder was set up at 10, 30, 50, 70, 100, 150, 200, 300, 400, and 500m from the hive. At each distance, I recorded 17 to 21 dances for each of the three colonies for a total of 572 dances from 171 bees; each dance had a minimum of 10 waggle phases (19 ± 8 , mean \pm SD). In a few cases (8%, 46 of 572), the data from two dances with fewer than 10 waggles phases were combined, provided they were performed by the same bee within 15 min of each other. All dances were recorded between 5 June 2005 and 10 August 2005, between 0800 and 1800 hours. Only one dance per bee per distance was recorded. Individual bees were often recorded at more than one distance. Waggle phases are seen in both the 'round' dance and the 'waggle' dance (personal observation; Kirchner et al., 1988; Jensen et al., 1997), as opposed to von Frisch's (1993) initial definitions. Therefore, all calculations are carried out in the same manner regardless of distance.

3.3.2 Data Transcription and Analysis

Data were transcribed with a Sony video tape deck (DSR-30) and monitor. The angle of each waggle phase was measured to the nearest degree using a protractor mounted on the monitor. The duration of each return phase was measured to the nearest 30th of a second using frame-by-frame playback. For each dance, the average

duration of the return phase was calculated. Many return phases were not followed by waggle phases, especially for nearby food sources. Therefore, return phase duration was measured only when there were waggle phases “bracketing” a return phase. To test the prediction of the brief-return phase hypothesis, I examined the effect of distance on return phase duration.

For each bee’s dance, I calculated the mean vector bearing (MVB) for her left and right waggle phases, and their variances, using equations found in Fisher (1993). Divergence angle is the absolute value of the difference between MVB_L and MVB_R (see Figure 3.1b). To investigate the brief-waggle-phase hypothesis, I looked at how the divergence angle and the variance within dances change with distance; both variables were log transformed to fit the assumptions of the analysis.

To investigate the tuned-error hypothesis, I looked at how patch radius, as inferred from dances, changes with distance. To estimate the size of the patch indicated in a dance, I calculated the patch radius as follows:

$$\text{radius of patch (r)} = d * \tan(\theta/2)$$

where d is the linear distance to the food source and θ is the divergence angle (see Figure 3.2). Within this equation, the one parameter that the bees are able to adjust is divergence angle. Therefore, I compare my data with a null model, in which divergence angle is held constant (calculated using the average divergence angle for all dances: 20°), to see the effects of the bee’s modifications of the dance form. In the statistical analysis, radius was square root transformed to satisfy the assumptions.

All variables were analyzed with a repeated-measures mixed-model ANOVA fitted with random intercept and/or random slope using PROC MIXED in SAS (Littell et al., 1996). For all variables, colony was modeled as a fixed effect and distance was examined for both linear and quadratic effects. Individual bees (dancers) were treated as subjects for repeated measures. Pairwise comparisons of variables between specific

distances were made where needed by using Tukey-Kramer post-hoc tests. Unless noted above, untransformed data satisfied all assumptions for the statistical tests.

3.4 Results

3.4.1 Return phase Duration

There is a marginally significant effect of colony on return phase ($F_{2, 185} = 2.90$, $P = 0.0574$), therefore, each colony's results are presented separately in Figure 3.3. Both the linear ($F_{1, 545} = 5.81$, $P = 0.0163$) and quadratic ($F_{1, 544} = 19.02$, $P < 0.0001$) effects of distance are significant, however, the interactions of colony with these effects of distance are not significant. The return phase duration generally decreases with food sources from 10 to 100 m and then increases from 100 to 500 m (Figure 3.3). Pairwise comparisons reveal that for all three colonies, return phase duration does not differ between dances for food sources at 10 m (1.56 ± 0.04 , mean \pm SE) and 400 m (1.56 ± 0.03); $t_{530} = 0.07$, $P = 0.9$). There is however, a significant difference between the return phase duration for food sources at 400 and 500 m (1.74 ± 0.03 ; $t_{485} = -3.98$, $P < 0.001$).

3.4.2 Divergence Angle and Variance

There is a significant colony effect on divergence angle ($F_{2, 230} = 4.06$, $P = 0.0185$), therefore each colony's results are presented separately in Figure 3.4. Both the linear ($F_{1, 546} = 13.57$, $P = 0.0003$) and quadratic distance effects ($F_{1, 540} = 4.26$, $P = 0.0395$) are significant, but the interactions of colony with those effects are not. Within each colony, the pattern of the change in divergence angle over distance is approximately the same: there is a sharp decrease with food sources from 10 to 50 m (divergence angle of approximately 20°), and then the slope changes and there is a slow but steady decrease until food source reaches 500 m (divergence angle of 10°).

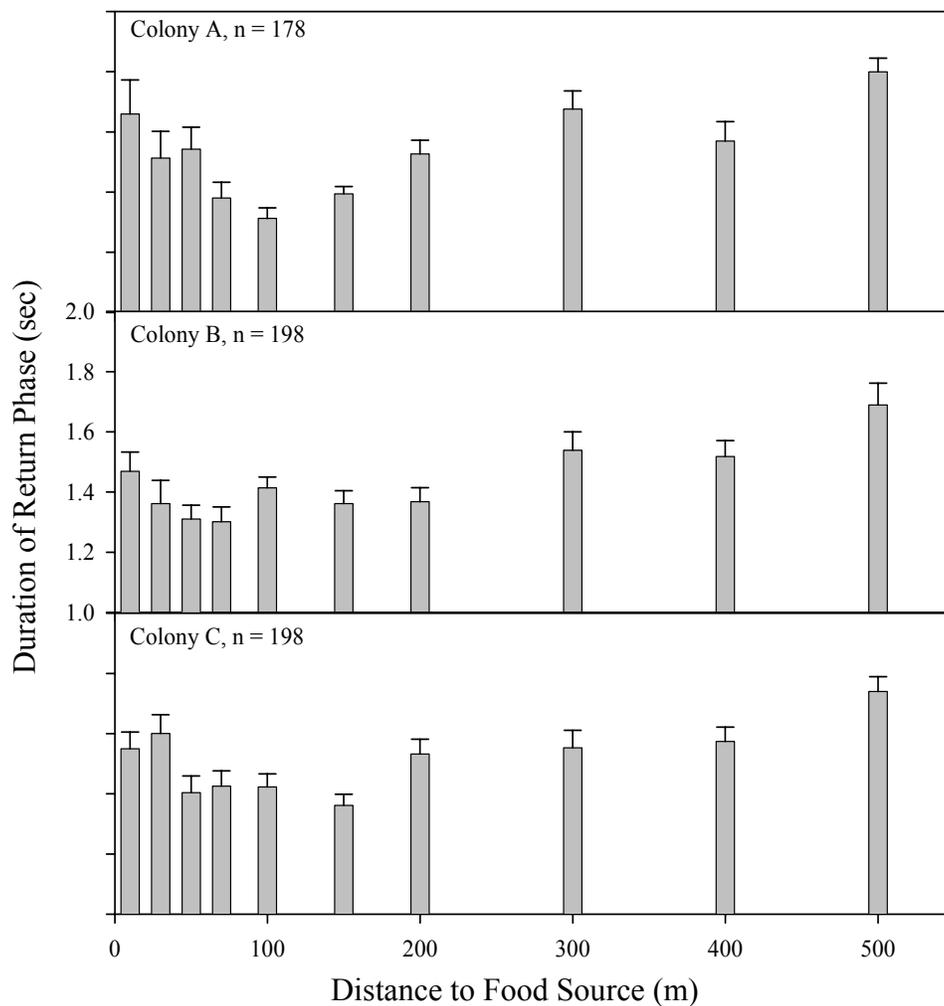


Figure 3.3 Distributions of return phase duration in relation to food-source distance. Each bar indicates the mean \pm SE; all y-axes are on the same scale. As distance of the food source from the hive increases, the duration of the return phase remains relatively constant. In each colony, the duration of the return phase has a significant quadratic relationship with distance to the food source, however, pairwise comparisons reveal that the return phase is not significantly different for nearby and distant food sources.

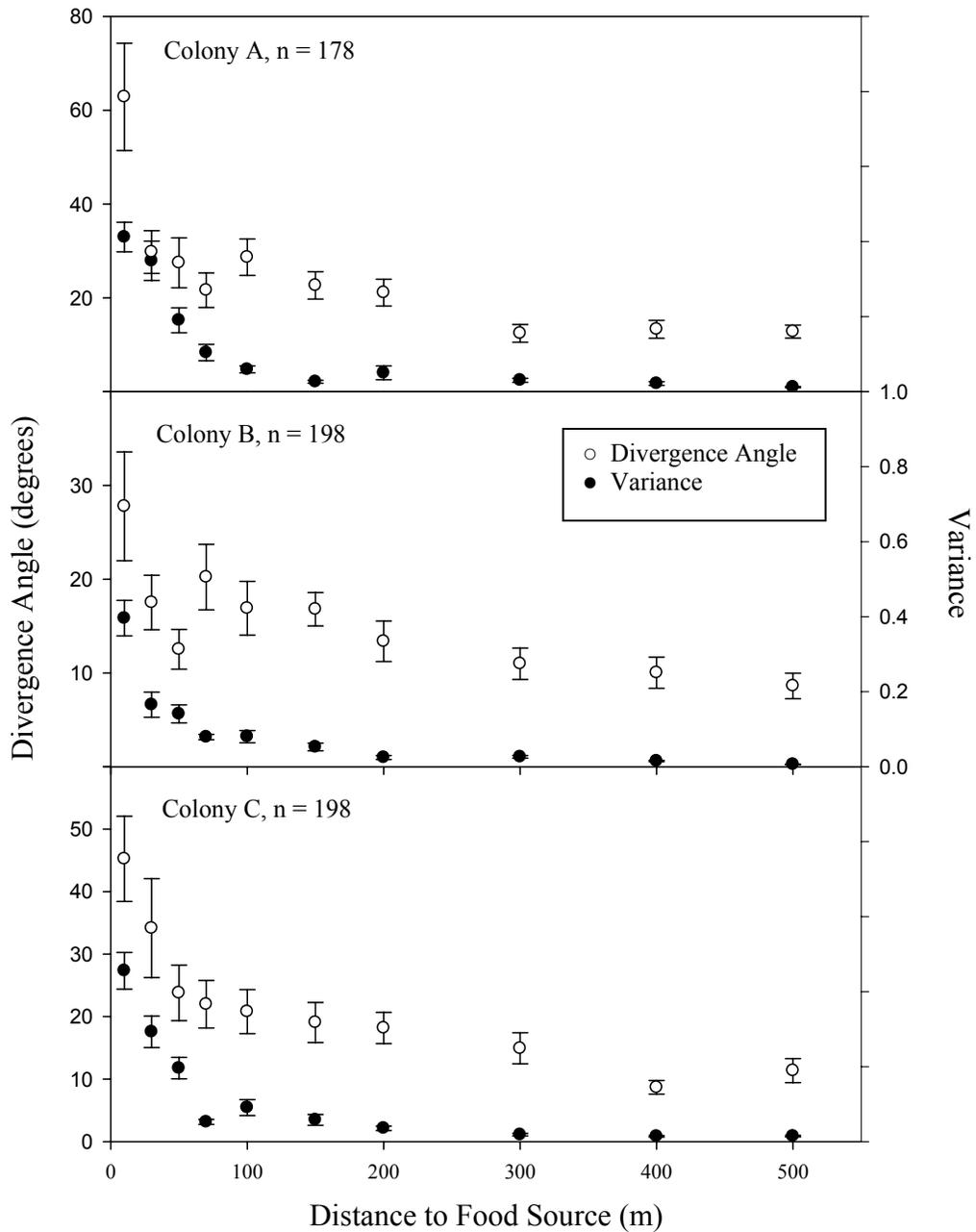


Figure 3.4 Divergence angle and variance in relation to food-source distance. Divergence angle: open circles, mean \pm SE, left y-axis; note difference in scales for each colony. Variance: closed circles, mean \pm SE, right y-axis; note same scale for each colony. Only variance in left waggle phases is shown; variance in right waggle phases had an identical pattern.

Variance of left and right waggles show the same pattern, for simplicity, only the results of left waggles are shown. There is no effect of colony on variance ($F_{2, 186} = 2.20, P = 0.1139$), but all colonies are presented separately in Figure 3.4. There are significant linear ($F_{2, 540} = 286.25, P = 0.0001$) and quadratic effects ($F_{2, 536} = 98.22, P = 0.0001$). The interaction of colony and quadratic distance effects is significant ($F_{2, 533} = 3.44, P = 0.0328$). All colonies show the same general pattern: variance of left waggle phases decreases rapidly as distance to the food source increases until about 70 m, beyond which point the variance decreases only slightly and slowly, eventually approaching zero at 500 m. Pairwise comparisons reveal that there is no significant difference in variance between food sources at 70 to 300 m, as well as between food sources at 150 to 500 m.

3.4.3 Advertised Patch Radius

There is a significant colony effect on patch radius ($F_{2, 453} = 4.94, P = 0.0076$). Both the linear ($F_{1, 536} = 123.18, P = 0.0001$) and quadratic distance effects ($F_{1, 515} = 39.44, P = 0.0001$) are significant, but the interaction of colony with those effects are not significant. All colonies show the same pattern (Figure 3.5): in dances for food sources less than 100 m from the hive, the radius increases in accordance with the null model. For food sources at distances greater than 100 m from the hive, the radius continues to increase slowly, but more slowly than predicted by the null model.

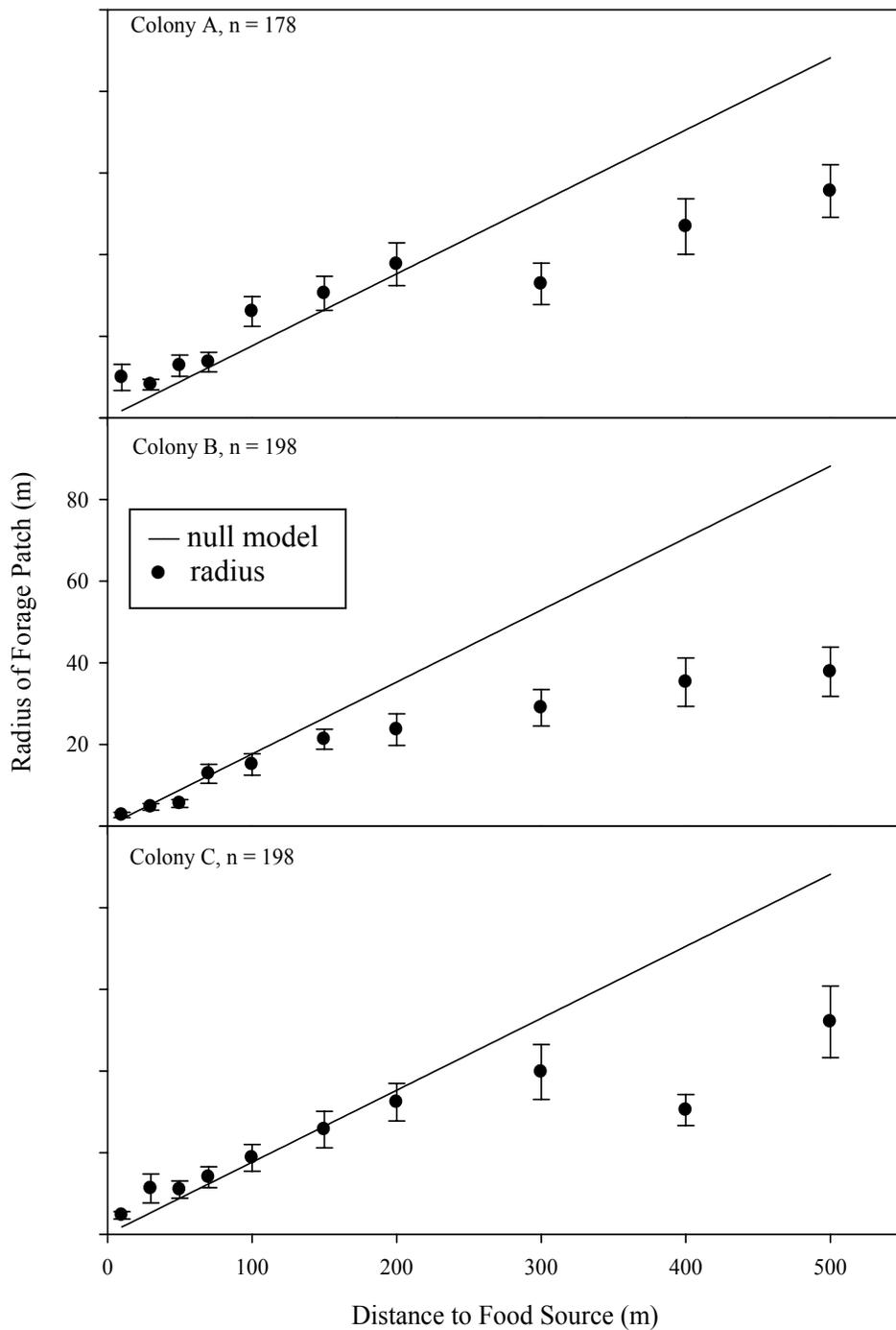


Figure 3.5 Forage-patch radius indicated in dances in relation to food-source distance. Radius was calculated using the equation given in text. The dots (mean \pm SE) indicate the patch radius, calculated from individual dances, while the solid line indicates a “null” radius, where divergence angle is held constant.

3.5 Discussion

The dance language of the honey bee is a complex form of communication that may maximize foraging efficiency at the colony level (Sherman and Visscher, 2002; Dornhaus and Chittka, 2004). A curious feature of this communication system is the occurrence of divergence angles for nearby food sources. There has been much speculation about why this imprecision exists, and why it varies as a function of food-source distance from the hive (e.g. Haldane and Spurway, 1954; Edrich, 1975; Towne and Gould, 1988; Weidenmüller and Seeley, 1999; Dornhaus, 2002; Beekman et al., 2005; Tanner and Visscher, 2006). Recently, Beekman et al. (2005) suggested that bees are, at least to some extent, constrained to producing low precision (high divergence angle) dances for nearby food sources because these dances have short return phases which give the bees little time to orient their waggle phases. My data do not support this ‘brief-return-phase’ hypothesis (see Table 3.1). A critical prediction of this hypothesis is that there will be a steady increase in return phase duration with increasing food-source distance. However, I found no significant difference in return phase duration between dances for food sources 10 m and 400 m from the hive, even though the precision of directional information is markedly less in dances for 10 m vs. 400 m. Beekman et al. (2005) reported a significant decrease in return phase duration as distance to the food source decreases. If one looks solely at dances for food sources greater than 100 m from the hive, as Beekman et al. did, this appears to be true. But if one looks at dances for less than 100 m, one sees that return phase duration actually increases with decreasing food-source distance. Because my results contradict the critical prediction of the brief-return-phase hypothesis, I reject this hypothesis.

A possible explanation of the positive relationship between return phase duration and distances greater than 100 m, as reported by Beekman et al. (2005), considers the geometry of the dance. If the waggle phase increases in duration (and

hence length), then it follows that the return phase must also increase in duration (length) because it simply takes longer for the bee to return to the starting position (see Figure 3.1). The unexpected pattern of increasing return phase duration as distance decreases for food sources less than 100 m may also be related to the geometry of the dance. Dances for food sources less than 100 m from the hive do not follow the typical figure eight pattern; as the consistency of the dance decreases with decreasing distance to the food source, return phase duration increases. Unintentional failure to see the short waggle phases in dances food sources less than 100 m from the hive may artificially increase the return phase duration. Although plausible, I believe this unlikely since frame-by-frame video analysis allowed for distinction of waggle phases as short as 10 ms.

A second non-adaptive explanation for the occurrence of large divergence angles in dances for nearby food sources is the ‘brief-waggle-phase’ hypothesis (see Table 3.1). It is well known that waggle phase duration is positively correlated with food-source distance (von Frisch, 1993), so one might suppose that dances for nearby food sources will have waggle phases so short that it is difficult for bees to successively align these waggle phases with high precision, giving rise to a large divergence angle. If this is true, then I should see that as food-source distance increases and thus waggle phase duration increases, then the directional scatter of waggle phases after left or right turns will decrease, indicating that bees are able to orient their waggle phases with increasing precision. My results indicate, however, that the bees are not constrained by short waggle phases to provide imprecise directional information. Specifically, the variance of waggle phase bearings after left or right turns is no greater in dances for 70 m food sources than in those for 300 m food sources. Likewise, the variance does not differ among dances for food sources at 150 m through 500 m. Concurrently, the bees are consistently decreasing the

divergence angle in dances for food sources at these distances. Hence, I conclude that the large decrease in divergence angle (between 70 and 500 m) cannot be explained in terms of increasing precision of waggle phase orientation due to increasing waggle phase duration. In rejecting the brief-waggle phase hypothesis, I assume that decreasing the divergence angle is physiologically no more difficult than decreasing the variance.

An interesting pattern emerges when one compares precision in dances for food sources (which typically exist as a diffuse patch) and potential nest sites (which are discrete points in space). Theoretically, dances for nest sites should have higher precision because there should be no adaptive value to spreading recruits around a point source. This is indeed the pattern reported by Weidenmüller and Seeley (1999), who found greater precision in dances for nest sites (performed on wire mesh) than in dances for food sources (performed on wax comb) at the same distances. However, in a subsequent experiment, Tanner and Visscher (2006) report no difference in divergence angle when dances for the two types of resource are performed on the same substrate (but this finding was not confirmed in an independent study; Seeley, unpublished data). This raises an additional possible explanation, where the availability of footholds influences precision; an excess of footholds, such as on wire mesh, may improve the bee's ability to orient waggle phases. Likewise, if a bee lacks sufficient footholds precision may be compromised. In my experiment, all dances were performed on natural wax comb, but availability of footholds may be related to the duration of the waggle phase. It is possible that a bee may be better able to secure good footholds when performing a longer waggle phase, which allows for more precise orientation. This would account for the decrease in variance as food-source distance increases, but not the maintenance of divergence angle at the food-source distances tested.

The third explanation for the occurrence of the divergence angle phenomenon is the tuned-error hypothesis: there is low directional precision in dances for nearby food sources because natural selection has favored imprecision within the dance language, resulting in the scattering of recruits. A prediction of this hypothesis is that the patch area indicated in dances will stay the same as distance to the food source increases. As with Towne and Gould (1988), I see a slight increase in the size of the advertised patch (as measured by the radius of the patch indicated within a dance) as food-source distance increases. However, after 200 m, this increase is less than predicted by the null model. The patch sizes found by Towne and Gould (1988) are larger than those that I report here (for example, approximately 9000 m² for a food source at 100 m compared to 1100 m²). This is most likely the result of differences in estimation methods. I report the geometric parameters of a patch indicated within a dance, whereas they reported the distributions of recruits in the field. Their spread of recruits should certainly be larger than my estimate since they are introducing at least two additional sources of error: recruit interpretation of the dance and recruit ability to fly precisely. An alternative measure of patch size might consider the spread of individual distance and direction points indicated by each waggle phase within a dance instead of looking at overall divergence angle.

My data show that patch size is not maintained at a constant size over distance, but increases as distance to the food source increases although divergence angle clearly decreases as food-source distance increases. However, since dancers have the ability to adjust divergence angle over wide ranges, it remains unclear as to why they do not decrease divergence angle at a greater rate as distance to the food source increases so as to keep patch size constant. There may be an adaptive value to spreading recruits out over slightly larger areas as distance increases, or perhaps the discrepancy in patch size is small enough that it makes no difference in overall

foraging efficiency, and no further selection for increased precision has occurred. Or there may be other, as of yet unexplored, constraints on the bee's ability to dance precisely for nearby food sources.

The ability to “tune error” may be most important in an evolutionary sense when food sources are farther from the hive (> 100 m). A relatively stable patch radius only after food sources greater than 100 m (Figure 3.5) suggests that precision within dances may be distance-dependent (Kirchner and Grasser, 1998; Dornhaus, 2002). There may be little selection pressure to indicate precise locations when food sources are nearby (< 100 m) since recruits may be able to find food sources quickly without highly accurate information.

In summary, I tested three hypotheses for explaining the imprecision that is present in the dance language of the honey bee (‘brief-return-phase,’ ‘brief-waggle-phase,’ and ‘tuned-error’). The brief-return-phase hypothesis is contradicted by the finding that there is not a steady increase in return phase duration as food-source distance increases. The brief-waggle-phase hypothesis is contradicted by the finding that the variance in waggle phase bearings after left or right turns falls to a constant and low level at distances when the divergence angle is still prominent. The evidence for the tuned-error hypothesis is less clear; although not perfect, the bees appear to be modifying the dance form in accordance with distance to the food source, indicating a relatively constant patch size within their dances for food sources within 500 m of the hive. This suggests that there may be an optimum spread to the scatter of recruits which has been tuned by natural selection according to local resource distributions, although ecological data on resource distribution would augment the interpretation of the tuned-error hypothesis.

CHAPTER 4

ACCURACY IN THE WAGGLE DANCE IN RELATION TO TIME OF DAY

4.1 Summary

The honey bee's dance language conveys information about the distance and direction of a rich food source from a successful to a prospective forager. An interesting phenomenon is that often there is error in the bee's directional information. Also, Karl von Frisch, the discoverer of the dance language, noticed that the bees reduce their foraging activity in the middle of the day, what he called "noontime laziness." Here I report that the level of accuracy within dances for food sources at 300, 400, and 500 m from the hive changes over the course of the day. Inaccuracy is highest during the middle of the day, when the sun is at its highest altitude. This suggests that sensing the sun's azimuth may be more difficult for the bees when the sun is higher in the sky. This also suggests an adaptive value to the reported reduction in foraging activity around mid-day because error within dances is highest during that time.

4.2 Introduction

The dance language of the honey bee transfers information about the location of a food source from a successful forager to prospective recruits, thereby increasing colony-level foraging efficiency (von Frisch, 1993). The typical dance is divided into two alternating phases, the waggle phase and the return phase. During the waggle phase, the bee shakes her abdomen vigorously from side to side (see Figure 3.1, page 25). The direction to the food source is communicated during the waggle phase: the angle of the waggle phase with respect to vertical is the same as the angle between the

food source and the sun's azimuth (the point on the horizon directly below the sun). Successive waggle phases may differ in orientation, but the mean bearing of all waggle phases indicates the direction to the food source.

Bees forage at all times during the day, even if the sun is only partly visible. An interesting phenomenon occurs with bees in the tropics: dance activity ceases when the sun is at the zenith, or an altitude of 90° (Lindauer, 1961). No directional information can be communicated when the sun is directly overhead. When encouraged to forage by providing a highly rewarding food resource, Lindauer (1961) reported that bees perform disoriented dances approximately 10 minutes before and after the sun is at the zenith. The effect of the sun's altitude on the bees' dance behavior confirmed that the sun is an essential element in the communication of direction. While the sun never reaches the zenith in the temperate zone, the extent to which the sun's position in the sky affects dance accuracy has not been investigated.

In the temperate region, von Frisch (1993) noticed that foraging activity decreases around noon, an observation he calls "noontime laziness." Although he attempted, he could not explain this lull in foraging activity in terms of an external factor, such as food profitability. He concluded is that the lull is an expression of a diurnal periodicity in activity, although this was not directly tested. Consequently, the cause of this decreased foraging activity is unclear.

Inaccuracy in the dance may be due to errors in acquiring directional information from the sun; as the sun rises in the sky, inaccuracy may increase. Therefore, I tested the hypothesis that accuracy of dances changes over the course of the day. I recorded dances for an artificial feeder at fixed locations throughout the day and transcribed the dances to determine the error in directional information and found that the highest inaccuracy occurs when the sun is highest in the sky.

4.3 Methods

4.3.1 Observation Hives

I recorded dances from three unrelated colonies (A, B, and C); A and C were housed in two-frame observation hives while B was housed in a four-frame observation hive. The size of the colony does not appear to influence dance behavior (Beekman et al., 2004). The specifications of the observation hives are described elsewhere (Seeley, 1995, ch. 4). To facilitate observations, I confined dances to a specific area of the comb by fitting each hive with a wedge that forced bees to enter on one side (Visscher and Seeley, 1982). Colonies were housed at two locations (A and C were together), within Ithaca, NY, USA W76° 29', N42° 26'.

4.3.2 Artificial Feeders and Recording Dances

The bees were trained to an artificial feeder of 0.5 to 2.0 M sucrose solution scented with anise oil (60 μ l/l) using the methods of von Frisch (1993, p. 17). Sugar concentration was varied and new recruits were captured to reduce crowding at the feeder, which can inhibit dancing upon returning to the nest (Fernández and Farina, 2002; Thom, 2003). Foragers were individually marked with paint (mixture of clear shellac and dry artist's pigment) and their dances were recorded upon their return to the hive.

Dances performed by marked bees were videotaped at 30 frames per second using a Sony mini-DV camcorder (DCR-TRV50). The feeder was set up individually at 300, 400, and 500 m from the hive. While there is may be a distance dependence on other aspects of the dance (see chapter 3), there was no difference in accuracy for these three food-source distances ($F_{2, 150} = 0.17$, $P = 0.8439$). At each distance, I recorded 19 to 21 dances for each of the three colonies for a total of 179 dances from 93 bees; each dance had a minimum of 10 waggle phases (19.7 ± 8.8 , mean \pm SD).

Only one dance per bee per distance was recorded but individual bees were often recorded at more than one distance. In a few cases (6%, 10 of 179), the data from two dances with fewer than 10 waggles phases were combined, provided they were performed by the same bee within 15 min of each other. All dances were recorded between 12 June 2005 and 21 July 2005, between 0815 h and 1615 h EST (all times corrected for daylight savings time). This time frame encompasses the summer solstice, the date that the sun reaches its highest altitude, on 21 June 2005 the sun reached an altitude of 71° at between 1201 h and 1214 h EST in Ithaca, NY.

4.3.3 Data Transcription

Data were transcribed with a Sony video tape deck (DSR-30) using frame by frame playback. For each dance, I recorded the angle of each waggle phase using a protractor mounted on the monitor with 0° as straight up. The angle from the hive to the feeders (θ_F) was the average of three independent readings using a sighting compass. The azimuth of the sun (θ_S) was determined from the U.S. Naval Observatory Web Site (Naval Observatory, 2006).

To calculate the angular error of each dance, I determined the difference between the observed and expected angles for each dance. The expected dance angle (θ_E) is the difference between the sun's azimuth and the direction of the feeder ($\theta_S - \theta_F$). The observed dance angle (θ_O) is the mean vector bearing of all waggle phases, calculated with equations found in Fisher (1993). The angular error is defined as the absolute value of $\theta_O - \theta_E$. The effect of the time of day on angular error was evaluated using a repeated-measures model with colony modeled as a fixed effect and time as a covariate with linear and quadratic components using PROC MIXED in SAS (Littell et al., 1996).

4.4 Results

For the timeframe of my recordings, the sun reached its maximum altitude of 67.9° to 71° between 1201 h and 1214 h EST in Ithaca, NY. The angular error of dances increased as the sun rose in the sky until about 1300 h and then it decreased as the sun lowered (Figure 4.1). Both the linear ($F_{1, 152} = 8.66$, $P = 0.0038$) and quadratic ($F_{1, 153} = 8.93$, $P = 0.0033$) terms in the model were significant. Colony, distance, and associated interactions were not significant ($P > 0.50$ for all terms). According to the quadratic fitted line, the highest imprecision within dances is at 1309 h.

4.5 Discussion

The sun is a useful directional reference, in that it is consistent and predictable, but it also presents problems since its location in the sky changes throughout the day. Therefore, bees must compensate by changing their dances according to the direction (azimuth) of the sun. This compensation is easily observed. If the location of a feeder is kept stationary, the waggle phases of the dance change orientation throughout the day in accordance with the position of the sun. Bees in the tropics perform extremely disoriented dances 10 minutes before and after the sun is at the zenith (Lindauer, 1961), which is most likely a consequence of the fact that the sun cannot provide directional information when it is directly overhead. While it is clear that the bee's eye is an excellent instrument for measuring solar cues, how its ability changes as the sun's location in the sky changes remains unresolved.

The highest angular error did not exactly correspond with the time of day when the sun is highest in the sky (Figure 4.1). There may, however, be no statistical difference between the peak of the best-fit quadratic curve and the actual time of day when the sun is the highest. It is also important to consider the mechanisms that bees use to compute directional information: the direct visual cues from the sun as well as

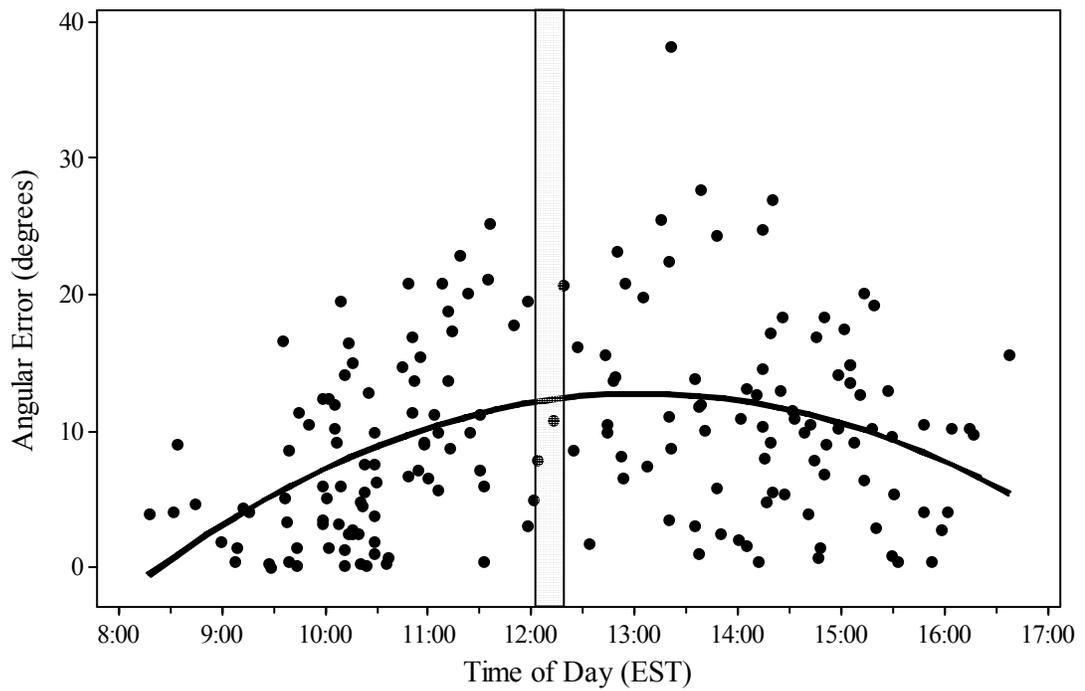


Figure 4.1 Inaccuracy in the dances of honey bees over the course of a day. The shaded area indicates the time during which the sun is at its highest altitude for the dates that dances were recorded. Inaccuracy increases as the sun rises in the sky and then decreases as the sun is setting, suggesting that it is more difficult for the bees to obtain directional information from the sun when it is higher in the sky.

the memory of the sun's position (Michener, 1974). When the sun is not in view, such as behind trees or clouds, bees use their memory of its past position to extrapolate its current position. The discrepancy may be due to the bee's extrapolation of the sun's current position; their calculations of the sun's position may not correspond exactly to the actual movement of the sun.

Although the highest angular error of the dances did not directly correspond with the time when the sun was highest in the sky, the pattern that I found (see Figure 4.1) suggests that bees have more difficulty in acquiring directional information from the sun when it is higher in the sky. Deviation from the expected waggle phase angle increased as the sun rose in the sky and then decreased as the sun set. It seems that the angular accuracy of dances is correlated with the altitude of the sun; bees are better able to communicate directional information if the sun is lower in the sky.

Von Frisch (1993) found that there is a lull in foraging activity in bees during the middle of the day. This "noontime laziness" is accompanied by an increase in the inaccuracy of directional information within dances; it may be that the reduction in foraging activity is adaptive. The dance language evolved to increase colony-level foraging efficiency. The observation that there is a decrease in foraging activity when there is an increase dance inaccuracy suggests that the dance language is truly optimized. The bees may reduce their foraging efforts when there is increased difficulty in transmitting accurate information to their nestmates.

CHAPTER 5

DO HONEY BEES HAVE TWO DISCRETE DANCES TO ADVERTISE FOOD SOURCES?

5.1 Summary

Honey bees use a complex dance language to communicate distance and direction to profitable food resources relative to the hive; arguably the most complex form of non-primate communication. In his Nobel Prize-winning discovery, Karl von Frisch decoded the system by which foragers convey these parameters after returning from a successful foraging trip. He described the ‘round dance’ and the ‘waggle dance.’ The round dance is used to indicate food sources close to the nest (less than 50 m) and is generally believed to contain no directional information. The ‘waggle dance’ is used for food sources more than 100 m from the nest and contains both distance and direction information. The concept of there being two discrete dances, i.e. two different terms in the dance language of honey bees, has been widely accepted since its inception in the 1920s. Surprisingly, however, there has never been a detailed examination of the behavioral parameters of dances over the range of distances represented by round dances and waggle dances. Here, I quantitatively show that the round dance and the waggle dance convey the same spatial information and that there is no abrupt switch between the two. Therefore, these results demonstrate that it is most meaningful to view the dances as representing different parts of a continuum and that the bees have a single adjustable recruitment signal: the waggle dance.

5.2 Introduction

More than 80 years ago, a discovery was made that changed the way we think of insects. Karl von Frisch described a system by which forager honey bees (*Apis*

mellifera L.) are capable of communicating location information about profitable food sources to their nestmates. This discovery was a pivotal advance in behavioral biology during the twentieth century; along with Konrad Lorenz and Niko Tinbergen, von Frisch is considered one of the founders of ethology (Alcock, 1998). Although the dance language has remained the subject of intense study to the present day (e.g., Michelsen, 1993; Dyer, 2002; Crist, 2004; Dornhaus and Chittka, 2004), as well as the subject of heated controversy (e.g., Gould, 1976; Robinson, 1986; Wenner and Wells, 1987; Crist, 2004), the view that there are two distinct “terms” in the dance language (round dances and waggle dances) has been widely accepted with little further inquiry ever since von Frisch drew the distinction between these two dance forms. Here, I present an examination of the round dance/waggle dance dichotomy and suggest that a revision in this conceptual framework may be necessary.

Through meticulous measurements and careful calculations, von Frisch and his students described the ‘waggle dance’ and the ‘round dance’ (von Frisch, 1993). The waggle dance typically has a figure-eight shape and conveys information about food sources farther than 100 m from the hive. It consists of two parts: the waggle phase and the return phase (see Figure 3.1, page 25). During the waggle phase, a bee dashes forward in one stride (Tautz et al., 1996) and vibrates her abdomen rapidly from side-to-side at approximately 15 Hz. The bee’s movement direction during the waggle phase contains directional information; the angle of the waggle phase with respect to gravity is the same as the angle of the food source with respect to the sun’s azimuth. The duration of the waggle phase communicates the distance to the food source; longer waggle phases indicate more distant food sources. After completing a waggle phase, the dancer performs the return phase by making a complete 360° turn to the right or left thereby bringing her back to the approximate place where the previous waggle phase began. Although the waggle phase contains the most spatial

information, the return phase may contain qualitative information about food source profitability (Waddington, 1982; Seeley et al., 2000).

Dances for nearby food sources (less than 50 m from the hive) are often somewhat irregular in form, with bees running in excited circles, turning both left and right, sometimes with a waggle phase and sometimes without. These dances, known as ‘round dances,’ are often thought to contain no directional information since early studies suggested that there is no directional orientation of the movements within these waggle phases of the round dance (see Jensen et al., 1997).

Von Frisch’s early work involved setting up a feeder near his observation hive and watching the dances the foragers performed upon returning to the hive. Initially, the only local food source was the experimental sugar water feeder such that all bees returning with nectar were performing irregular dances, while bees returning with pollen were performing well-formed figure-eight-shaped dances. Von Frisch’s initial conclusion was that dance form was related to resource type – bees foraging for nectar performed ‘round dances’ and bees foraging for pollen performed ‘waggle dances’ (von Frisch, 1971). Although he eventually realized his error and acknowledged that dance form was not related to food source but rather to distance, his initial interpretation may have paved the way for the persistent belief that there are two separate dances:

“It was clear that the round dance and the wagging dance are two different terms in the language of the bees, the former meaning a source of food near the hive and the latter a source of food at 100 meters or more” (von Frisch, 1971, p. 91).

Waggle phases are accompanied by a 200-350 Hz buzz produced by wing vibrations (Wenner, 1962), which vary linearly with distance to the food source (Spangler, 1991). These buzzes generate air currents sufficient to stimulate the

Johnston's organ in the antennae and evidently transmit information about the duration of the waggle phase and perhaps also about the orientation of the dancer's body (Michelsen et al., 1987). Kirchner et al. (1988) report that acoustic signals give information about direction in the round dance in the same manner as in the waggle dance. This finding is the first report in which the round dance and the waggle dance were equated in their inclusion of information about resource location. Kirchner et al. (1988) state that direction is indicated acoustically for food sources 1 m from the hive, an impressive finding considering that it was previously believed that direction was only indicated, although imprecisely, for food sources greater than 50 m from the hive.

More recently, Jensen et al. (1997) showed that waggle phases statistically indicate direction for food sources greater than 15 m from the hive and suggest that Kirchner et al.'s findings were an overestimation because of averaging the direction of many waggle phases. Here, I report findings on the distance and direction components of waggle phases and take a systematic approach to comparing the two dance forms. I investigated the occurrence of distance and direction information, which many have thought is contained only in waggle dances, by looking at dances for 10 food-source distances, ranging from 10 m to 500 m from the hive. I found that both distance and direction information is indeed present in round dances as well as waggle dances, suggesting that the round dance and the waggle dance are really just two variants of the same signalling behavior, although there is certainly more signal noise in dances for nearby, relative to distant, food sources.

5.3 Methods

Three unrelated colonies (A, B, and C) were maintained in observation hives, as described by Seeley (1995, ch. 4). Working with one colony at a time, I trained foragers to a sugar water feeder at 10 distances, 10, 30, 50, 70, 100, 150, 200, 300,

400, and 500 m, according to the methods of von Frisch (1993, p. 17). The dances of individually marked bees were recorded upon their return to the hive. I recorded 15 to 21 dances per colony per distance (572 dances total) using a Sony mini-DV camcorder (DCR-TRV50). Only one dance per bee per distance was recorded, but an individual bee was sometimes observed and recorded at more than one distance. Feeders were supplied with 0.5 to 2 M sucrose solution scented with anise (60 μ l/l). Sucrose solution concentration was adjusted to have a high, but not overwhelming, level of dancing for the feeder. Only 5-10 bees at a time were allowed to visit the feeder, to prevent overcrowding there (Fernández and Farina, 2002; Thom, 2003). All dances were recorded from 5 June 2005 to 10 August 2005 between 0800 and 1800 hours and contained a minimum of 10 waggle phases. However, in a few cases (8%, 46 of 572) data from two dances with fewer than 10 waggles were combined provided they were performed by the same bee within 15 minutes of each other.

Since distance is indicated by the duration of the waggle phase, I calculated the average waggle phase duration to the nearest 30th of a second for each dance. Waggle phase duration was analyzed using a mixed model repeated-measures ANOVA in SAS (Littell et al., 1996). Colony was modeled as a fixed effect, distance was examined for both linear and quadratic effects, and individual bees (dancers) were treated as subjects for repeated measures. To investigate the relationship between waggle phase duration in the ‘round’ and ‘waggle’ dances, I divided the data into two groups based on food-source distance, 10 to 100 m and 100 to 500 m. 100 m is considered the beginning of the waggle dance (von Frisch, 1993) and was included in each group.

Directional information is conveyed by the angle of the waggle phase, which was recorded with 0° as straight up and normalized to the ‘expected angle,’ the difference between the sun’s azimuth and the feeder angle. This generated a circular distribution of the deviations of the observed waggle phase angle from the expected

dance angle (i.e., 0° indicates that the angle of a waggle phase matched the expected dance angle). Circular histograms were created by grouping all waggle phases within each distance for each colony, as in Jensen et al. (1997). Mean vector bearing (MVB) is the average direction of all waggle phases. Mean vector length (MVL) is a measure of spread in the circular data and can be considered a ‘goal-oriented component’ for each dance (referred to as ‘ r ’ in Jensen et al. (1997) and Kirchner et al. (1988)). MVB and MVL were calculated for each colony at each distance using equations found in Fisher (1993). Rayleigh’s z -test was to test for directionality with the null hypothesis that the circular distribution of all angles comes from a uniform circular distribution (Fisher, 1993). Circular histograms and Rayleigh’s z -test were calculated using Oriana v. 2.02.

5.4 Results

5.4.1 Distance Information

Waggle phases were present in all recorded dances for food-source distances less than 100 m from the hive (Figure 5.1), although only dances (individual or the amalgamation of two) with more than 10 waggle phases were analyzed. There was a significant effect of colony on waggle phase duration ($F_{2, 147} = 8.73, P = 0.0003$), therefore all colonies are presented separately in Figure 5.1 and Table 5.1. There was an overall significant linear ($F_{1, 210} = 80.63, P < 0.0001$) and quadratic ($F_{1, 198} = 21.56, P < 0.0001$) effect of distance. The interactions of colony with both the linear ($F_{2, 208} = 3.77, P = 0.0247$) and quadratic ($F_{2, 196} = 3.81, P = 0.0239$) distance components were significant. In all colonies, the linear coefficient (β_1x) was highly significant, and the quadratic coefficient (β_2x^2) was significant in colonies B and C, but not A (Table 5.1).

Although there was no significant effect of colony on waggle phase duration for food-source distances of 100 to 500 m ($F_{2, 258} = 1.23$, $P = 0.2934$), all colonies are presented separately in Figure 5.1 and Table 5.2. There was an overall significant linear ($F_{1, 286} = 212.70$, $P < 0.0001$) and quadratic ($F_{1, 263} = 26.60$, $P < 0.0001$) effect of distance on waggle phase duration, although the interaction of colonies with each of these is not significant ($P > 0.12$). In all colonies, the linear coefficient (β_1x) was highly significant and the quadratic coefficient (β_2x^2) was significant in colonies A and C, but not B (Table 5.2).

5.4.2 Directional Information

To facilitate comparisons, I plotted directional data in the same manner as Kirchner et al. (1988) and Jensen et al. (1997). For all distances examined, waggle phases showed a directional preference (MVL is significant) and scatter decreased as distance increased (larger values of MVL; Figures 5.2, 5.3, 5.4). For all colonies at all distances, the goal-oriented component, MVL, was significant, indicating that the distributions of waggle phases are not from a random circular distribution (Rayleigh's z -test, Tables 5.3, 5.4, 5.5). There was a directional preference in dances for food sources as close as 10 m to the hive.

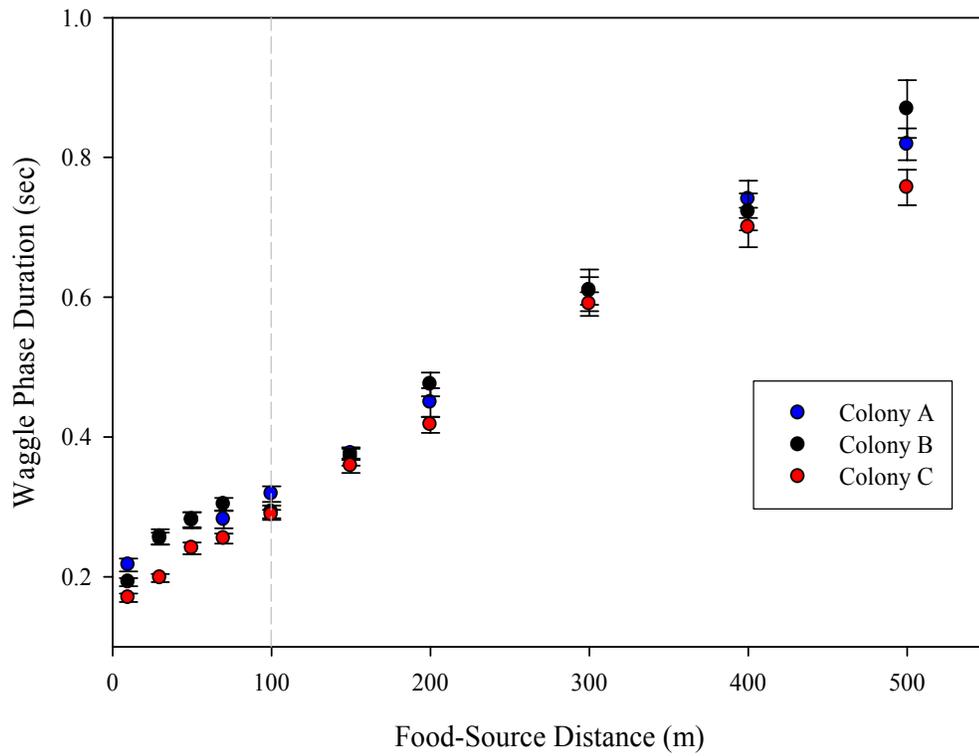


Figure 5.1 Waggle phase duration for 3 colonies, mean \pm SE, $n = 572$, dashed line indicates the presumed beginning of the ‘waggle dance’. Distance is encoded in the ‘round dance’ in the same manner as in the ‘waggle dance’.

Table 5.1 Parameter estimates for waggle phase duration for food-source distances 10 to 100 m, the ‘round dance.’

Colony	Parameter	Estimate \pm SE	<i>t</i> statistic	<i>P</i> value
A	Intercept	0.209 \pm 0.026	$t_{145} = 4.08$	$P < 0.0001$
	β_1x	0.015 \pm 0.005	$t_{219} = 3.14$	$P = 0.0019$
	β_2x^2	-0.0004 \pm 0.0004	$t_{210} = -1.02$	$P = 0.3072$
B	Intercept	0.1626 \pm 0.026	$t_{150} = 1.19$	$P = 0.2372$
	β_1x	0.0325 \pm 0.004	$t_{204} = 7.41$	$P < 0.0001$
	β_2x^2	-0.0018 \pm 0.0004	$t_{197} = -4.92$	$P < 0.0001$
C	Intercept	0.1449 \pm 0.011	$t_{147} = 13.53$	$P < 0.0001$
	β_1x	0.0224 \pm 0.004	$t_{191} = 5.18$	$P < 0.0001$
	β_2x^2	-0.0008 \pm 0.0004	$t_{176} = -4.92$	$P = 0.0303$

Table 5.2 Parameter estimates for waggle phase duration for food-source distances 100 to 500 m, the ‘waggle dance.’

Colony	Parameter	Estimate \pm SE	<i>t</i> statistic	<i>P</i> value
A	Intercept	0.112 \pm 0.069	$t_{257} = 1.07$	$P = 0.2868$
	β_1x	0.020 \pm 0.003	$t_{280} = 8.09$	$P < 0.0001$
	β_2x^2	-0.0001 \pm 0.00004	$t_{264} = -2.85$	$P = 0.0048$
B	Intercept	0.1284 \pm 0.067	$t_{257} = 1.52$	$P = 0.1294$
	β_1x	0.0176 \pm 0.002	$t_{291} = 7.55$	$P < 0.0001$
	β_2x^2	-0.00006 \pm 0.00003	$t_{273} = -1.57$	$P = 0.1183$
C	Intercept	0.06822 \pm 0.028	$t_{257} = 2.45$	$P = 0.0150$
	β_1x	0.0221 \pm 0.002	$t_{284} = 9.71$	$P < 0.0001$
	β_2x^2	-0.0002 \pm 0.00003	$t_{249} = -4.61$	$P < 0.0001$

Figure 5.2 The indication of direction in the waggle phases of the dances in colony A. Statistical information for each circular histogram is provided in Table 5.3. For all distances, the directional component is significant ($P < 0.01$). Direction is indicated within ‘round dances’ and ‘waggle dances.’ The angle of the red arrow indicates the MVB and the length of the red arrow indicates MVL. The black solid line is the direction of the food source.

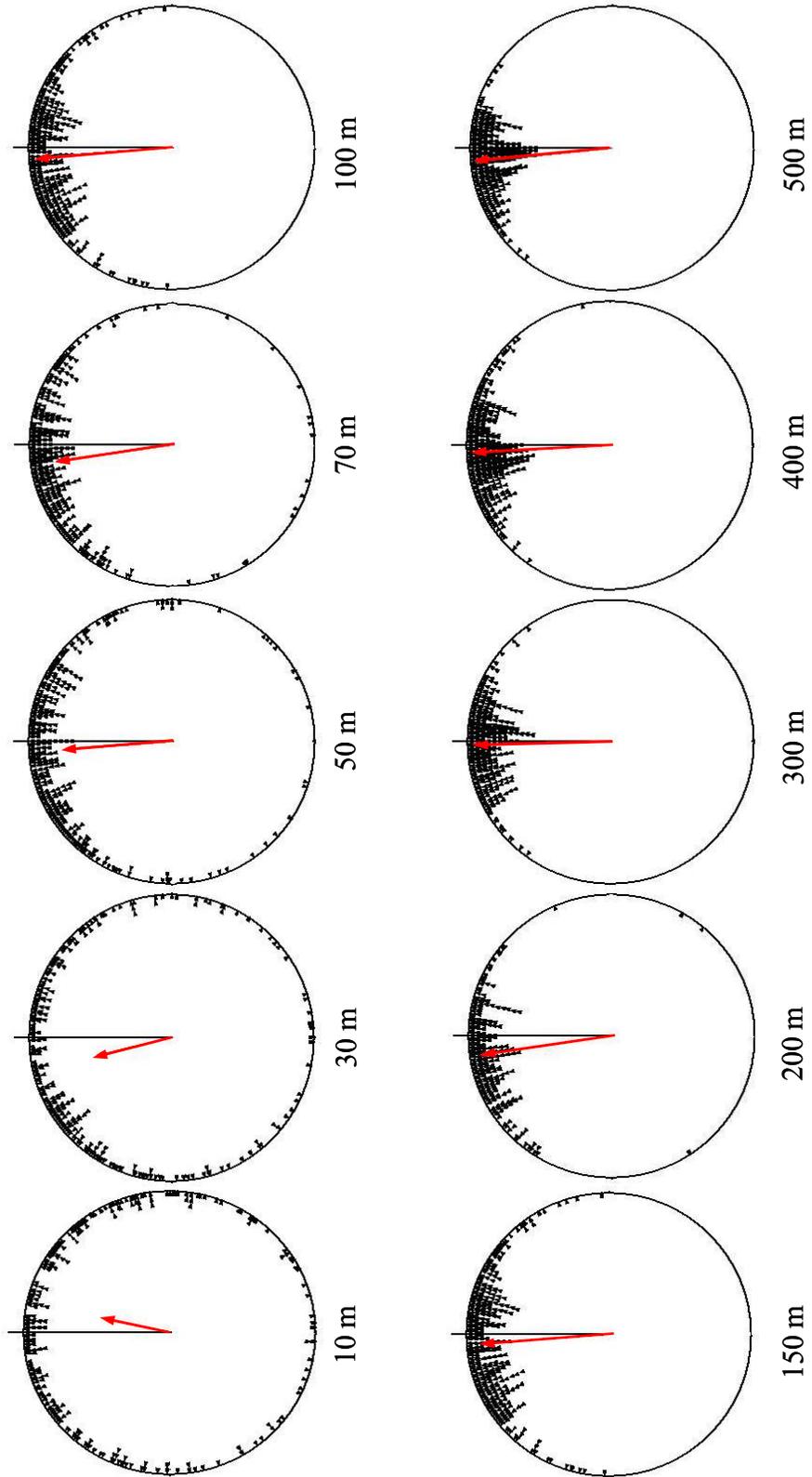


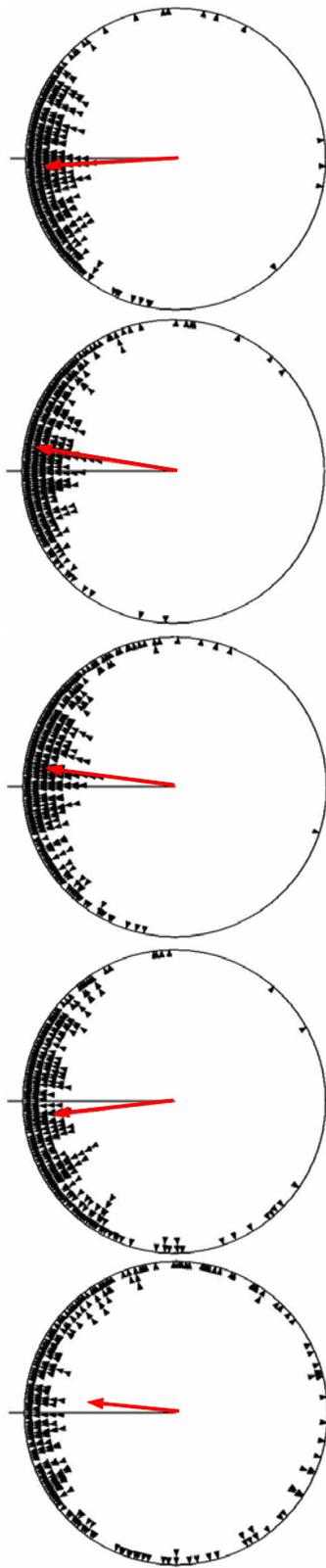
Table 5.3 Circular statistics for dances at 10 food-source distances for Colony A.

Distance	10	30	50	70	100	150	200	300	400	500
n (waggles)	246	248	313	322	322	263	227	283	327	288
Dances [†]	17	15	17	20	17	18	16	19	20	20
MVB	11.85°	-13.6°	-4.0°	-8.4°	-4.3°	-3.5°	-8.6°	-1.3°	-3.1°	-4.3°
MVL	0.447	0.530	0.733	0.811	0.887	0.936	0.918	0.954	0.949	0.962
Rayleigh's Test (z) [‡]	49.11	69.67	168.32	211.58	253.38	230.63	191.35	257.66	294.69	266.58

[†] The number of dances equals the number of dancers at each distance

[‡] All are significant at $P < 0.01$

Figure 5.3 The indication of direction in the waggle phases of the dances in colony B. Statistical information for each circular histogram is provided in Table 5.4. For all distances, the directional component is significant ($P < 0.01$). Direction is indicated within ‘round dances’ and ‘waggle dances.’ The angle of the red arrow indicates the MVB and the length of the red arrow indicates MVL. The black solid line is the direction of the food source.



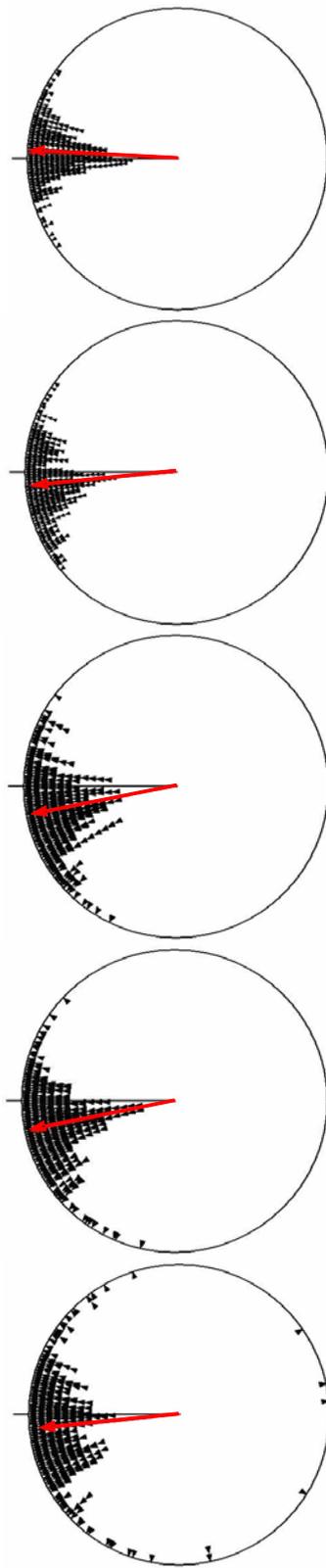
100 m

70 m

50 m

30 m

10 m



500 m

400 m

300 m

200 m

150 m

Table 5.4 Circular statistics for dances at 10 food-source distances for Colony B.

Distance	10	30	50	70	100	150	200	300	400	500
n (waggles)	288	325	350	339	342	350	341	335	341	350
Dances [†]	20	18	20	20	20	20	20	20	20	20
MVB	6.8°	-6.7°	8.3°	8.8°	-3.9°	-6.1°	-11.9°	-10.7°	-5.1°	2.3°
MVL	0.544	0.791	0.850	0.879	0.864	0.906	0.959	0.956	0.969	0.982
Rayleigh's Test (z) [‡]	88.5	203.1	252.6	261.8	255.4	287.1	313.5	306.5	320.1	337.2

[†] The number of dances equals the number of dancers at each distance

[‡] All are significant at $P < 0.01$

Figure 5.4 The indication of direction in the waggle phases of the dances in colony C. Statistical information for each circular histogram is provided in Table 5.5. For all distances, the directional component is significant ($P < 0.01$). Direction is indicated within ‘round dances’ and ‘waggle dances.’ The angle of the red arrow indicates the MVB and the length of the red arrow indicates MVL. The black solid line is the direction of the food source.

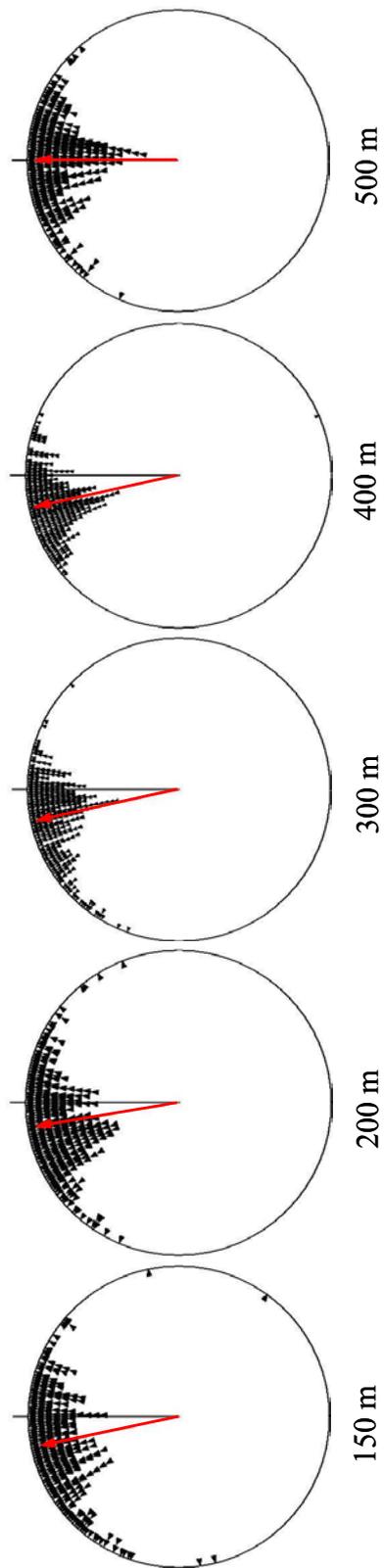
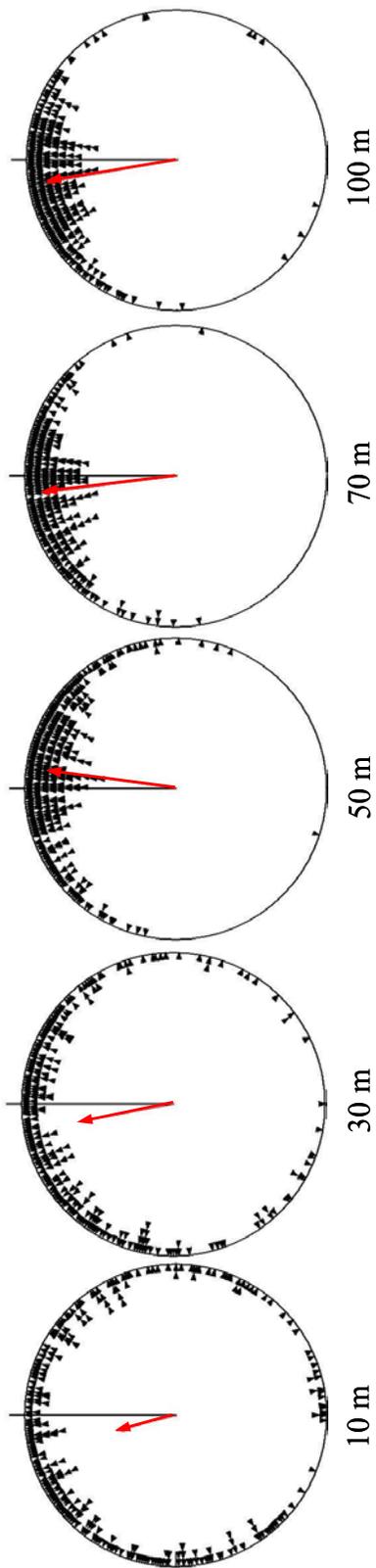


Table 5.5 Circular statistics for dances at 10 food-source distances for Colony C.

Distance	10	30	50	70	100	150	200	300	400	500
n (waggles)	294	280	350	301	320	323	340	350	340	346
Dances [†]	19	18	21	20	20	20	20	21	20	19
MVB	-14.1°	-10.6°	8.8°	-7.4°	-9.7°	-12.1°	-9.7°	-12.3°	-12.6°	2.3°
MVL	0.404	0.605	0.85	0.895	0.877	0.916	0.942	0.959	0.971	0.951
Rayleigh's Test (z) [‡]	48.08	183.0	230.1	251.4	249.8	260.8	272.0	283.2	301.3	279.6

[†] The number of dances equals the number of dancers at each distance

[‡] All are significant at $P < 0.01$

5.5 Discussion

Since its initial discovery by Karl von Frisch, the honey bee's dance language has captivated scientists from a range of disciplines. Furthermore, the initial terminology put forth by von Frisch to describe this communication behavior has held strong. This chapter investigates the existence of two forms of the dance, what von Frisch called the round dance and the waggle dance. Currently, it is believed that these two forms are separate "words" in the language of the bees. However, I suggest that a revision to this terminology is needed because the round and waggle dances are merely two ends of a continuum. Distance and direction are encoded using the same mechanisms in both forms.

This is the first report of the linear relationship between waggle phase duration and distance for round dances (Figure 5.1), and of the similarity of the parameter estimates of waggle phases in the 'round dance' (Table 5.1) and the 'waggle dance' (Table 5.2). There is no discontinuity in waggle phase duration between dances for nearby and distant food sources, and distance is encoded in the same manner for food sources less than 100 m from the hive and greater than 100 m from the hive. The slight differences between colonies, giving rise to significant colony effects, may be attributed to genetic differences (Arnold et al., 2002; Johnson et al., 2002).

The presence of waggle phases in the round dance was described by von Frisch and others (see Jensen et al., 1997), however, it was believed that there was no directional information within them. The relation between waggle phase duration and food-source distances from approximately 100 m up to 10,000 m from the hive is well documented (von Frisch, 1993). Here, I extend those findings and show the continuity of the linear relationship by providing a detailed analysis of food sources between 10 and 500 m from the hive.

Kirchner et al. (1988) report significant directionality for food sources 1 m from the hive using the same statistical test, Rayleigh's z -test. However, their results were based on the average waggle angle within complete dances, each containing dozens of waggle phases, which artificially reduces scatter (increases MVL). This method of calculation presumes that potential foragers are capable of following dances more or less completely and 'calculating' a mean vector. Although the means by which follower bees gather information are not fully understood (Judd, 1995), this scenario is unlikely given that individual dances can contain up to 200 waggle phases (Seeley, 1995) and bees following the dance typically attend fewer than 10 waggle phases (Judd, 1995). My results are congruent with those of Jensen et al. (1997), which show significant directionality for food sources at 15 m from the hive.

An interesting pattern emerges in the circular histograms, there appears to be a left-directed bias in the waggle phases (negative MVB). Although unlikely, this could be the influence of an artificial light source outside the hive to which the bees are orienting during their dance. Or, perhaps the dancers are compensating for the fact that recruit bees will be flying to the goal when the sun is in a slightly different position than on the initial flight, which would introduce a bias to the left of the expected orientation.

The large amount of 'noise' (small MVL) in dances for nearby food sources evidently led to an initial conclusion there is no directional information within the 'round dance,' as described by von Frisch (1993). However, the present examination of the distance and direction components within the dance shows that they are encoded in the same manner for all distances. The signal-to-noise ratio merely decreases as distance decreases (see Kirchner et al., 1988). This indicates that the bees have only one adjustable dance that encodes distance and direction to the food source, but that the expression of this information is distance-dependent.

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