

GLADYS JULIETH CASTIBLANCO QUIROGA

MULTISCALE ANALYSIS OF EUSOCIAL TRAFFIC DYNAMICS

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Doctor Scientiae*.

Orientador: Og Francisco Fonseca de Souza

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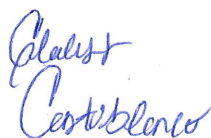
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Dedicatória

To my inspirers: termites, those beings individually frail but collective powerful.

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Resumo

CASTIBLANCO QUIROGA, Gladys Julieth, D.Sc., Universidade Federal de Viçosa, novembro de 2020. **Multiscale analysis of eusocial traffic dynamics**. Orientador: Og Francisco Fonseca de Souza.

A diferença do trânsito em sistemas humanos, o trânsito de insetos sociais parece fluido e estável. Aqui, testamos a estabilidade de tráfego do *Constrictotermes cyphergaster* com o objetivo de conhecer as causas do trânsito fluido nestes animais. Nossos resultados indicam que os padrões formados no nível de colônia (a escala macroscópica) são consequência das interações interindividuais (a escala microscópica). Em particular, nossos resultados indicam que a estabilidade do tráfego de cupins é uma consequência dos movimentos co-ordenados (cooperativos) que emergem de interações interindividuais inibitórias. Além disso, mostramos que um ciclo inverso de luz, temperatura e umidade relativa pode redefinir o ritmo de forrageamento de térmitas noturnos que forrageiam à céu aberto. Nosso protocolo foi altamente eficaz para induzir forrageamento durante o dia.

Palavras-chave: Forrageio. Dinâmica de trânsito. Cupim.

Abstract

CASTIBLANCO QUIROGA, Gladys Julieth, D.Sc., Universidade Federal de Viçosa, November, 2020. **Multiscale analysis of the eusocial traffic dynamic.** Advisor: Og Francisco Fonseca de Souza.

Different from human traffic, the traffic of social insects seems highly smooth and stable. Here, we tested the traffic stability of *Constrictotermes cyphergaster* aiming to know the causes behind their smooth traffic. Our results indicate that the patterns formed at the colony level (the macroscopic scale) are a consequence of inter-individual interactions (the microscopic scale). In particular, our findings indicate that the stability of termites' traffic is a consequence of the coordinated (co-operative) movements which emerge from inhibitory interindividual interactions. In addition, we showed that an inverse cycle of light, temperature, and relative humidity can reset the foraging rhythm of nocturnal open-forager termites. Our protocol was highly effective to induce foraging during the day.

Keywords: Foraging. Traffic dynamics. Termites.

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Chapter 1

General Introduction

Contrarily to the breakable car traffic of human societies, traffic created by social insects like ants and termites is highly smooth. Knowing the causes behind the stability of that organized traffic could open the possibility of applying some principles in human systems. In this work, we inspected the stability of termites' foraging trails and studied their causes.

In human systems, breakdown traffic is common with a high impact on the economy. For example, in Barcelona, the cost of traffic jams for 2003 was €367 million ([García-Altés and Pérez, 2007](#)). The self-interests of humans above the collective interests seems to be the cause of such traffic instabilities. [Helbing \(1992\)](#) found that departures of human pedestrian traffic from a highly fluid flow rise from the intentionality of individuals within the stream. Walking or driving at the desired speed, adjusting speed to their own goals like arriving at a certain hour, and anticipating interactions such as collisions and acting to avoid them, are examples of intentionality.

Possibly the most impressive case of group behaviour is eusociality. Insects such as ants and termites are eusocial, whose individuals have lost the ability to survive alone. Individuals in these insects have reached absolute specialization of the reproductive functions ([Oster and Wilson, 1978](#)) as occurs with the cells of the human body. As such, individuals who search for food or defend the nest are unable to reproduce, and those who can repro-

duce are unable to search for food or defend the nests. In eusocial groups, individuals behave highly coordinated like cells and the entire group as an individual (Oster and Wilson, 1978). The eusocial condition, hence, may make traffic flows immune to self-interest in such insects. Here, we showed for the first time some features of termites' traffic, focus on the behavioral basis of their smooth flow.

1.0.1 Model species

C. cyphergaster is a Neotropical termite species distributed in South America (Seevers, 1957; Mathews, 1977), particularly in the Central and Southeastern "Cerrado" (Constantino, 1998) and in the Northern "Caatinga" (Melo and Bandeira, 2004) biome of Brazil; Paraguay, Bolivia, Northern Argentina (Constantino, 1998). *C. cyphergaster* termites construct their nests above the soil on trees or rocks (Vasconcellos et al., 2007). In this species, there is a linearly relation between the nest volume and the size of population; the soldiers : workers proportion is 1:3 (Vasconcellos et al., 2007). The nest of *C. cyphergaster* harbour many arthropods ranging from other termites species like the obligate inquilines of the genera *Inquilinitermes* (Constantino, 1998) to rove beetles highly specialized to termitarium life of genera *Corotocha*, *Spirachtha*, and *Termitocola* (Seevers, 1957).

C. cyphergaster termites forage forming exposed columns up to 18 m of length mobilizing thousands of individuals (Moura et al., 2006a). This termite species is a central place forager that uses a mix of trail pheromone and fecal pellets to create long-term foraging trails (Moura et al., 2006a) functionally similar to the trunk-trails created by leaf-cutting ants (Bochynek et al., 2019). Soldiers protect the foragers, the individuals of this caste stop and guard at the lateral of the trails. Foraging duration is of ≈ 7 hours, usually starting close at 22:00 h and finishing at 5:00 h (Moura et al., 2006b). However, at the collection site we observed termites' columns returning to

the nest between 6:30 h and 7:00 h. Individuals of *C. cyphergaster* feed on the bark of live trees, wood in different decomposition phases (Moura et al., 2006b), and lichens (Barbosa-Silva et al., 2019). Termite workers of this species carry the food to the nest in their gut (Moura et al., 2006b) and some of them also transporting pellets of food on their mandibles (personal observations). The trails formed by *C. cyphergaster* have reproductive importance to the termitophile *Corotoca melantho*. Females of this rove beetle leave the nest following the foraging trails of their host and deposit the larvae on the back of termite workers (de Oliveira et al., 2018).

1.1 Overview of chapters

This thesis is divided into three chapters, this is the first of them. This chapter is a general introduction to the main topic of this thesis, the description of the biological model, and an overview of chapters. The main experiment of this work is based on the foraging behaviour of *C. cyphergaster*. However, this termite species forage at night and that poses problems to data collection. So in chapter 2, we showed a simple and effective protocol to induce foraging at laboratory conditions during the day. In chapter 3 we inspected the stability of termites' traffic at two scales: (i) macroscopic, to observe the effect of the width of foraging platforms on the flow formation; and (ii) microscopic, to search in the inter-individual interactions the causes of the macroscopic pattern found. At the macroscopic scale, we didn't register traffic jams in response to platform variation. However, we found a drop in some parameters of the foraging process with increments of the platform width. In wide platforms, as opposed to narrow ones, termites: (i) ate less, (ii) walked more, (iii) reversed more often their walking direction, (iv) arriving less at the foraging arena, and (v) faced more often a lower number of head-on encounters. At the microscopic scale, we found that the head-

on encounters (collisions) between individuals modulate some important properties of termites' traffic. Increments in the number of collisions faced by termites resulted in: (i) a low probability to reverse the walking direction, (ii) a low propensity to halt in the trails, (iii) a non-linear regulation of the mean speed. We also found that the speed and the collision's dynamic changed with the time elapsed from the beginning of foraging. We argued that the absence of traffic jams is a result of the coordinated (co-operative) movements which emerge from inhibitory interactions.

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Chapter 2

**An effective method to reverse
nocturnal foraging rhythm in
open-forager termites (Blattodea:
Isoptera)**

Abstract

Circadian cycle is an endogenous clock present in living beings controlling their activities every 24 h cycle. This explains, for instance, why humans are mainly diurnal while organisms, such as *C. cyphergaster* termites, forage at night. Circadian cycles, therefore, may turn data collection on these termites into a challenging process. As with most circadian cycles, the foraging activity of this termite species is susceptible to external cues, such as temperature and relative humidity fluctuations. Natural variation in weather hence, adds an extra difficulty to data collection, because in the field the moment to start foraging is unpredictable. Aiming to propose an effective lab protocol to circumvent data collection problems, we tested if a reversed light, temperature, and relative humidity cycle could reset the foraging rhythm in *C. cyphergaster* termites. We compared the foraging activity between termite colonies with natural and reverse cycle. We found that the reverse light, temperature, and relative humidity cycle reset the foraging rhythm. Termite colonies with reverse cycle started to forage c.a 5 hours after the artificial darkness onset (11:13) following the same pattern to the colonies with natural cycle (c.a 5 h after real darkness onset - 22:57). In addition, behavioral observations revealed that the foraging activity preserved their naturalness in the reverse cycle. In brief, our protocol seemed effective, easily replicated, and accurate in inducing the foraging behaviour of nocturnal termite species under reversed daily cycle at lab conditions.

key words: Circadian rhythm, Foraging, *Constrictotermes cyphergaster*, Reverse foraging rhythm.

2.1 Introduction

Circadian (from Latin *circa* “around” and *diem* “day”) cycle refer to an endogenous metabolic “clock” responsible for the regulation of the 24 h cycle of an individual (Brady, 1974). Circadian rhythms represent adaptive advantages for individuals, since food availability, climatic conditions, and predator activity commonly follow a 24 h cycle (Helfrich-förster et al., 1998). However, the adaptive advantage of circadian cycles often leads to difficulties in data collection of nocturnal species. *C. cyphergaster* termites forage at night in open columns for ≈ 7 h, this termite species forage every ≈ 2 days but their exit of the nest depends on the temperature and relative humidity conditions (Moura et al., 2006). Thus, the use of *C. cyphergaster* as a biological model for foraging related studies have two important problems: their nocturnal activity and the unpredictability of the moment of foraging starting. Here we propose a simple lab protocol to circumvent those problems.

Foraging related studies are highly relevant from the theoretical and applied point of view. Many theoretical aspects of foraging remain partially unveiled as the drivers of foragers’ decision-making (Lehue and Detrain, 2020). In recent years, scientists have paid attention to the foraging of animals as a model for highly applicable studies as swarm robotics (Talamali et al., 2020), computational algorithms (Song et al., 2020), optimal designs for escaping in panicking conditions (Shahhoseini and Sarvi, 2017), and traffic dynamics (John et al., 2009). For all those cases, termites can be an excellent biological model, but their cryptic habits may pose challenges to data collection.

Circumventing some of these challenges appear promising, though. Circadian cycles, for instance, are highly susceptible to external cues such as sunlight, temperature, or relative humidity (Brady, 1974). Hebrant (1970)

discovered a respiratory circadian rhythm at colony level in *Cubitermes exiguus* termites, which was regulated by temperature and relative humidity fluctuations. Later, some authors have reported daily feeding rhythms in termites regulated by temperature. [Cornelius and Osbrink \(2011\)](#) showed that the subterranean termite *Coptotermes formosanus* forage when the soil temperature is $\geq 15^{\circ}\text{C}$. Also, [Lewis et al. \(2013\)](#) found that the feeding-related acoustic signals of the dry-wood termites *Incisitermes minor* are positively related to temperature. Surprisingly, even unpaired termite alates searching by a mate seems regulated by a daily rhythm in response to the light cycle ([Mizumoto et al., 2017](#)).

Such a dependence on external cues suggests that by inverting those daily cycles, it is possible to reset the nocturnal foraging rhythm of colonies of *C. cyphergaster* hence easing data collection (after all humans are mainly diurnal!). Here, we tested that hypothesis aiming to propose a method to reverse the nocturnal habits of nocturnal open-forager termites.

2.2 Methods

2.2.1 Sampling, Ethics Statement

We used as biological model *C. cyphergaster* (Blattaria: Isoptera: Termitidae: Nasutitermitinae) termites. 24 nests with no sign of damage were collected in the “Cerrado” Brazilian Biome in the Rural District of São José das Lajes, Municipality of Cordisburgo (S19°2', W44°15'), State of Minas Gerais, Southeastern Brazil. In total, we made two expeditions, the first from 17th to 19th June 2018; the second from 6th to 8th September 2018. The climate of the study area corresponds to Cwa (humid Subtropical, with dry winter and hot summer) in the Köppen system ([Alvares et al., 2013](#)). The minimum and maximum temperature registered for June was 9.7°C - 29.7°C with a mean of 19.1 °C, and for September was 8.6°C - 32.4°C with

a mean of 22.1 °C; the precipitation during the two study periods ranged from 0.0 mm to 0.2 mm and from 0.0 mm to 14 mm, respectively ([Instituto Nacional de Meteorología, 2020](#)). The sample and experimental activities reported here were exempt of any specific permission. O. DeSouza holds a permanent permit from IBAMA (The Brazilian Institute for the Environment and Renewable Natural Resources) to collect termites. Neither protected species were sampled nor genetical information was accessed.

2.2.2 Overall rationale

Here we tested if termites can change their natural periods of foraging in response to a temperature, humidity, and light inverse cycle. To do so, we performed a foraging experiment with two groups of termite colonies. The first group, called natural, was maintained at laboratory conditions without regulation of temperature, humidity, or light. The second group was exposed to a reverse cycle of temperature, humidity, and light; in which the nights were warmer, less wet, and more lighted than the day. We compared the foraging response between the two groups.

2.2.3 Nest maintenance in laboratory conditions

Termitaria with no sign of damage were removed from the field, put into plastic bags, labeled, and taken to the lab. Once there, nests were placed in plastic boxes covered with a small pore voile fabric to permit the exchange of gases and prevent the entrance of undesired arthropods. Five nests were kept in the lab, at room temperature and relative humidity. The other 19 nests were kept in a rearing room with controlled temperature and humidity. The temperature at the rearing room was modulated to oscillate between ≈ 21 and $\approx 28^{\circ}\text{C}$ with a 12:12 D:L photoperiod. Untreated drinking groundwater was provided *ad libitum* for termites in water-filled

test tubes closed by a piece of cotton. Tree bark, lichens, moss and pieces of filter paper were offered *ad libitum* as food. The food and water-tubes were changed every two days.

2.2.4 Experimental setup, data collection

To test the foraging activity at natural and reverse cycle, we connected the nest to a foraging arena using a platform (fig. 2.1). The platform was constructed with styrofoam and fixed to the boxes with silicone glue. Before connecting the system, the nests were exposed to a starvation period of three days. Only four test tubes filled with water were offered during starvation. On the day of the experiment, the foraging box was supplied with ≈ 1.5 g of pieces of filter paper, ≈ 22.5 g of wet lichen, moss, and tree bark, and four test tubes filled with water. The ground of the box was covered with a previously (1 day before) heat-treated soil at 111°C for 2 hours. For natural cycle, we used a platform of 5 cm width and 40 cm length. For the reverse cycle nests, we used a platform with the same 40 cm length and width variable (see Chapter 3 for a full explanation).

Before we moved the nest, the temperature of the experimentation room was adjusted to have the same conditions of the rearing room for reverse cycle colonies. Colonies with natural cycle were assayed in the rearing room of them (uncontrolled temperature and relative humidity). For both natural and reverse cycle assays, the connection to the foraging box was opened during the day at $\approx 7:00$ h. For natural cycle nests, we evaluated at every 1 hour the activity of the nest registering the hour of observation, the temperature, the activity inside the nest box, the activity in the platform, and the activity in the foraging box. For reverse cycle nests, we evaluated the same parameters every 30 min because those nests were more active. Observations in all assays ended when the first foraging bout was recorded. For nests under natural cycle, observations ended at 23:30h if no foraging

bout was recorded. If the latter happened, we restarted observations the next day between 5:00 and 6:00 h.

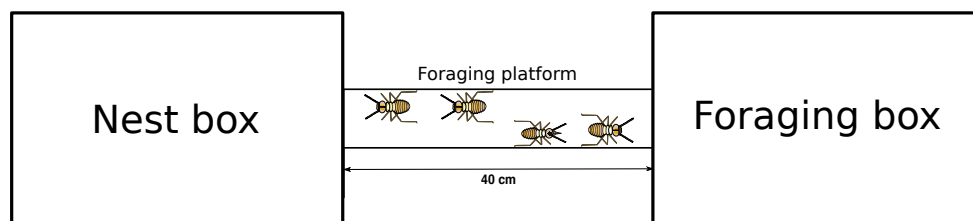


Figure 2.1: Experimental setup.

In addition, for the reverse cycle nests, we registered the caste composition of the exploring group, performed behavioral observations, and recorded the presence of arthropod symbionts in termite trails, along with any other remark on the naturalness of the foraging.

2.2.5 Induction of the reverse daily foraging rhythm

We exposed 19 *C. cyphergaster* colonies to a reversed daily temperature and humidity oscillatory period (figure 2.2). This was achieved by cooling the rearing room at daytime (06:00 to 18:00 h) and heating it at night (18:00 to 06:00 h), using an oil-filled electric heater (De'Longhi MG15T tm). The nests were exposed to the reverse temperature and humidity cycle for at least two weeks before the day of the assay. In addition we induced a reverse photoperiod of 12:12 D:L in the rearing room switching lights on at 18:00h and off at 06:00h.

2.2.6 Statistical analysis

To compare the two protocols used to induce foraging we analysed how quickly termite colonies started the foraging from the darkness onset. To do so, we used the censored survival analysis under Weibull distribution (Crawley, 2012), carried out in R (R Core Team, 2020) using the survival package (Therneau, 2020). In this analysis, the time origin was the darkness

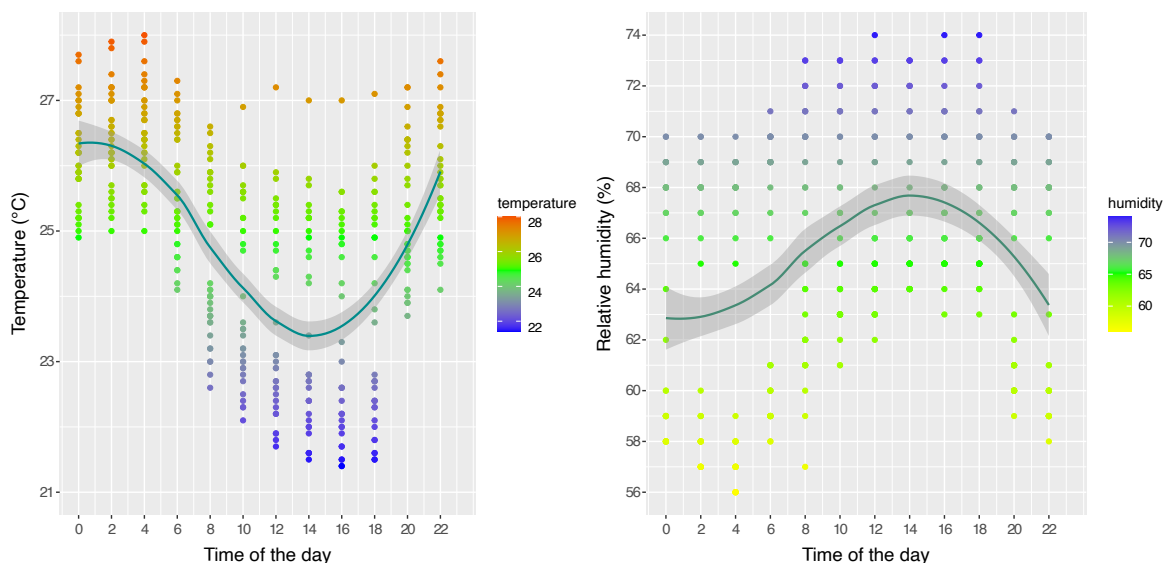


Figure 2.2: Daily temperature and humidity variations used to reverse the circadian cycle of *C. cyphergaster* termite nests.

onset and the end-point was the moment at which termites started the foraging episode in minutes. For termite colonies with natural cycle the darkness onset was at 18:00 (0 min). In the case of reverse colonies cycle, the darkness onset corresponded to 6:00 (0 min). The explanatory variable was the cycle with two levels: natural and reverse. We used p-value as a method for model selection with differences being accepted at $P < 0.05$.

2.2.7 Mean duration of foraging

To calculate the mean duration of the foraging episode of colonies exposed to reverse cycle, we used the censored survival analysis under Weibull distribution (Crawley, 2012). Here, we used the moment when foraging started as the time origin and the moment of its cessation as the endpoint. A censoring status variable assumed value $c = 0$ when that colony did not stop foraging after the period of observation (23:00 h) and $c = 1$ otherwise.

2.3 Results

2.3.1 Daily foraging rhythm

All colonies subjected to a reverse daily cycle of temperature, humidity, and light did reverse their foraging rhythm, foraging at daytime as we have hypothesized. Additionally, colonies subjected to reverse cycle started foraging 5:23 h after the onset of darkness while the colonies in the natural cycle started 4:55 h after (fig. 2.3 tab. 2.1).

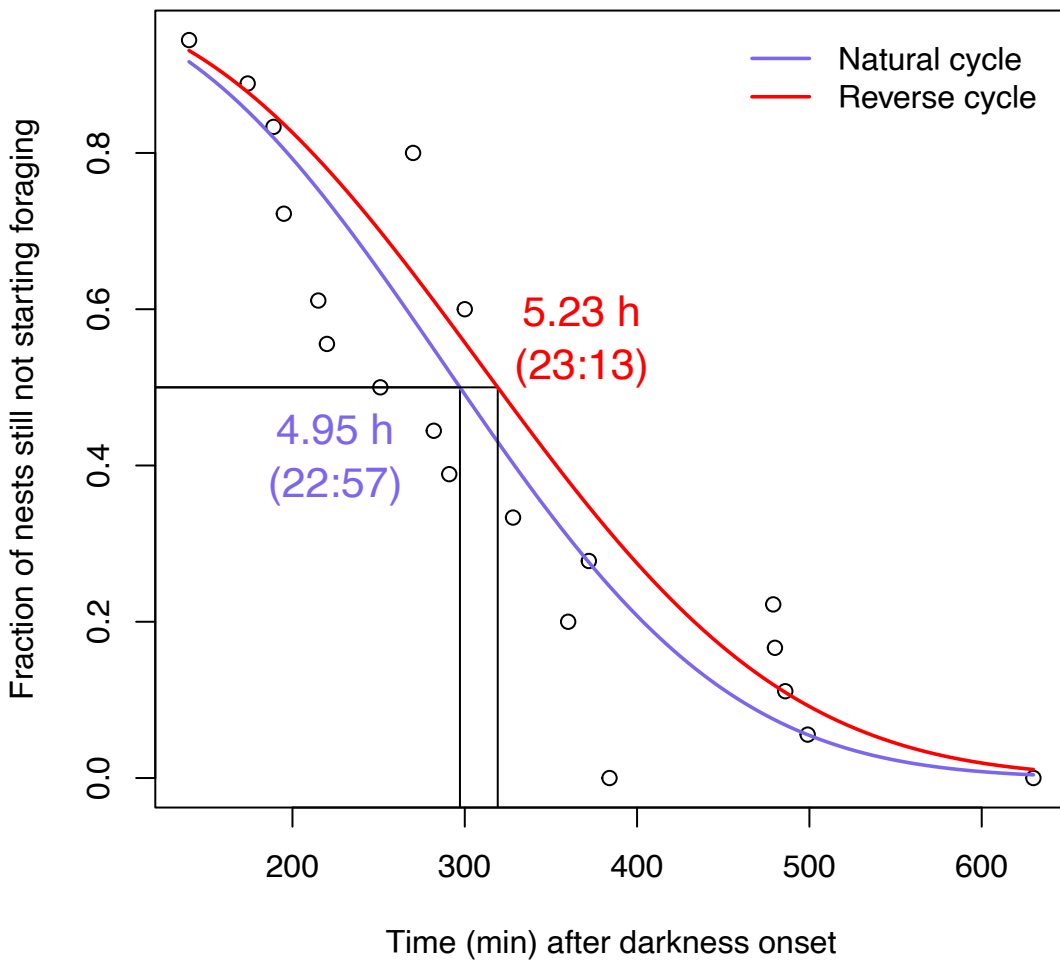


Figure 2.3: The fraction of nests still not started foraging as a function of the time (min) after darkness onset.

Table 2.1: Model selection to inspected the effect of the cycle on the mean time (min) after the darkness onset at which foraging occurred. Column headings: Loglik(model) = log-likelihood of the alternative model, df = degrees of freedom, Residual df = residual degrees of freedom, χ^2 = value of the Chi-squared test, p-value = p-value of the contrast between null and alternative model.

Null model: Time (min) \sim 1					
Alternative model : Time (min) \sim cycle					
Loglik(model)	df	Residual df	χ^2	p-value	n
-142.9	1	22	0.14	0.71	23

2.3.2 Observations on foraging of *C. cyphergaster* at laboratory conditions

We consistently observed that termitaria exposed to reverse cycle started foraging releasing a group mainly composed of soldiers. At this phase, soldiers walked slowly in a zig-zag pattern. The soldier-worker proportion was 10:1 at the phase of exploration. Sometimes workers alone left the nest but this did not result in nestmate recruitment. In all the colonies evaluated (natural and reverse cycle) there was a formation of soldiers at the lateral of the trails. Soldiers faced outwards, with the longer axis of their body perpendicular to the trails. That formation started \approx 46 min after the beginning of foraging. The formation of soldiers at the laterals always started from the ends of the trail towards the center (fig. 2.5). In all the colonies tested (natural and reverse cycle), soldiers were the last to enter the nest as foraging ended. Close to the end of foraging, soldiers performed many travelings between the nest and the foraging arena before complete retiring. *C. cyphergaster* formed bidirectional trails, however, there was no fixed position (center or laterals) for inbound or outbound termites. The termitaria exposed to reverse cycle foraged on average 10.20 hours (fig. 2.4). Also, were observed interactions between *C. cyphergaster* termites and their obligatory termitophile *Corotoca melantho* in the trails of colonies in

reverse cycle. In 5, individuals of *Corotoca melantho* left the nest and along with outgoing termites in foraging trails as described by.

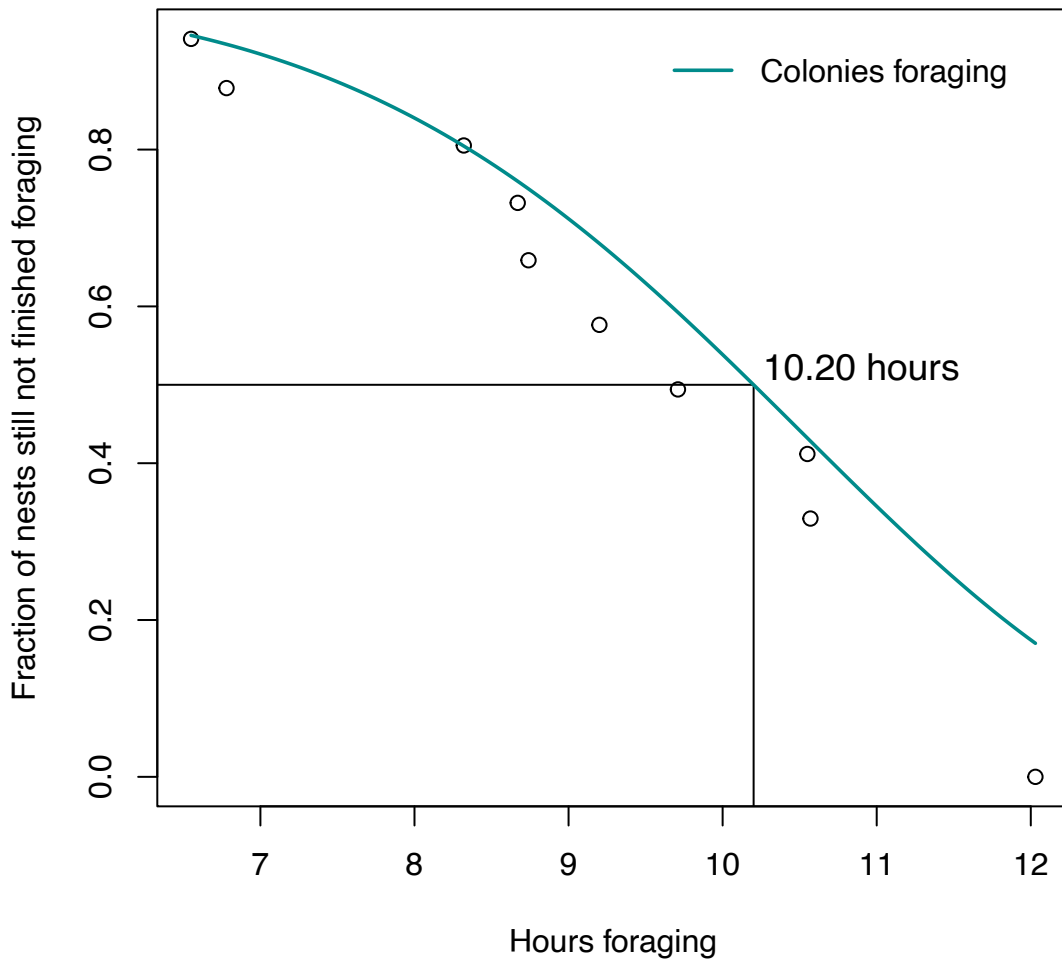


Figure 2.4: Foraging duration of colonies with reverse circadian cycle. The mean duration of foraging was 10.20 hours.

2.4 Discussion

Our results indicate that *C. cyphergaster* termite colonies exposed to a reverse temperature, humidity, and light cycle reset their natural foraging periods, confirming our hypothesis. Termites in the reverse cycle started to forage on average at 23:13 of the artificial night, the same period reported here for colonies in natural cycle ($\chi = 0.14$, $df_{red} = 23$, P-value = 0.71). The two protocols (natural and reverse) were effective in inducing foraging after a starvation period (all the tested colonies foraged). On top of easing

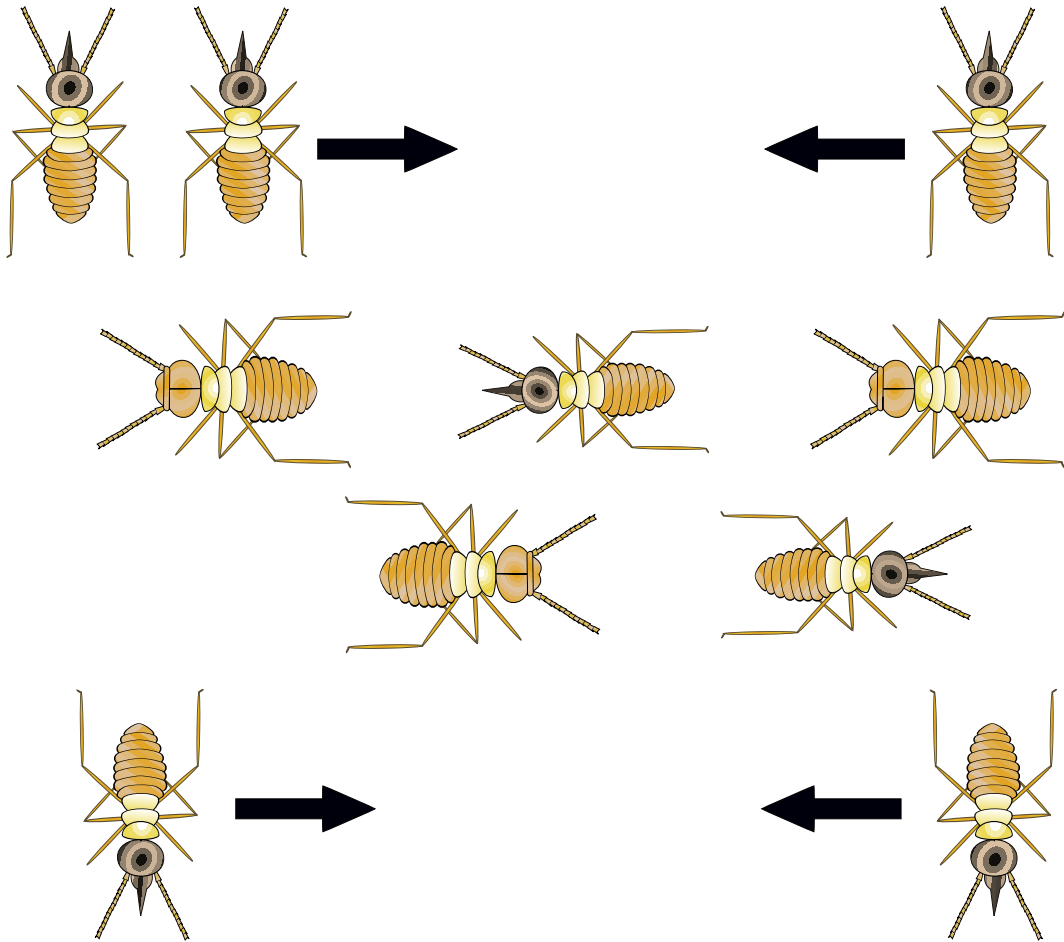


Figure 2.5: Formation of escort soldiers. The formation started from the ends towards the center of trails (arrows) ≈ 46 min after the foraging beginning.

the execution of foraging experiment at daytime with a nocturnal termite species (fig. 2.3, tab. 2.1). Probably, there is a physiological mechanism behind the reset of the foraging rhythm in *C. cyphergaster*. The existence of two genes related to the daily cycle of feeding activity in termites seems to validate that hypothesis. The first is the *deviate* gene for trail-following behaviour, which is responsive to photic conditions, temperature, and starvation (Schwinghammer et al., 2011). 24:0 and 12:12 L:D cycles increased the expression of *deviate*, as well as temperature $\leq 22^\circ$ (Schwinghammer et al., 2011). The second one is the foraging *for* gene, with high expression in the same light conditions as the trail-following gene, and at temperatures of 27° . It is possible, that those genes could participate as molecular switches in the foraging circadian rhythm of *C. cyphergaster*. Studies aiming to unveil the physiological mechanism of the foraging circadian rhythm in termites are needed.

In addition, the individuals from all termites colonies with reverse cycle exhibited consistent foraging behaviour (see 2.3.2), as previously reported for field colonies. We registered that a group mainly composed of soldiers started the foraging of *C. cyphergaster*, the same pattern observed by Moura et al. (2006) for this species in the field. 50% of the reverse cycle colonies started to forage at 11:13 which correspond to 23:13 in the artificial night, the same feeding rhythm of this species in the Caatinga (51% at 22:00 in the dry, 39% at 23:00 in the wet season) (Moura et al., 2006). Also, the duration of the foraging in reverse cycle colonies was very close (10.20 h) to the reported in field conditions in the Caatinga Biome (≈ 7 h) (Moura et al., 2006).

We observed in 5 reverse cycle colonies, *C. melantho* females and males rove-beetles walking in the middle of termite trails during the first two hours of foraging. This species is known for having an intimate symbiont interaction with *C. cyphergaster* termites. *C. melantho* beetles use the nest of

C. cyphergaster as reproductive site (Pisno et al., 2019), and have morphometric (da Cunha et al., 2015) and chemical (Rosa et al., 2018) resemblance with their termites host. Interestingly, *C. melantho* females use the *C. cyphergaster* termite foraging trails to deposit and disperse their larvae. Thus, the presence of *C. melantho* in trails of inverse cycle termite colonies indicates that our laboratory protocol preserved even this delicate inter-specific interaction.

We predict that the lab protocol proposed here can be adjusted for other nocturnal and open forager termite species. The simplicity and the quickness in response (2 weeks) make this method a good candidate to test the possibility of reverse foraging rhythm in other species. This protocol could lead to discovering many hidden aspects of termites foraging behaviour from the process itself to interactions with other arthropod species.

Beyond synchronicity and the faithfulness to reproduce at laboratory conditions the natural foraging behaviour of nocturnal termites, our protocol is also economically suitable. An oil-filled electric heater and a lighting system with a timer are relatively inexpensive and available in most labs with basic or middle infrastructure.

2.5 Concluding remarks

Data collection of nocturnal species lead to some limitations and difficulties. Here, we proposed for the first time a simple lab protocol to reverse the nocturnal foraging rhythm of an open-forager termite species. Our assays with *C. cyphergaster* termites colonies showed that: (i) a reverse cycle of temperature, relative humidity, and light reset the foraging rhythm, (ii) colonies with reverse cycle forage during the day facilitating data collection, and (iii) the inverse cycle preserves the naturalness of foraging behaviour and delicate symbiotic inter-specific interactions. Also, the pro-

protocol proposed is inexpensive and reliable available. Concluding, our lab protocol seemed simple, effective, easily replicated, and accurate in inducing the foraging behaviour of nocturnal termite species at lab conditions.

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Chapter 3

Multiscale analysis of eusocial traffic dynamics

Abstract

Traffic is distinctive of some societies ranging from foraging insects to humans' complex rule-based vehicle flow. Termites are known to have impressive smooth traffic without the need for central control. The cause of such differences is a hot topic in traffic and complex systems theory. Here we tested the stability of termites' traffic flow to know the mechanism behind their smooth traffic. We examined the effect of the width of the foraging platform on the traffic dynamic of *C. cyphergaster*. We tested seven platform widths. For assays, we connected the whole colony to the foraging arena through a platform. We recorded the full foraging episode (each c.a 10.2 hours long) of 18 different nests and manually tracked 3700 focal termites. We analyzed termites' traffic at two scales: macroscopic, to know the outcome at the collective level and microscopic to inspect the cause of the macroscopic pattern at the individual level. At the macroscopic scale, we found that the platform width did not provoke jams or significant congestion. However, we observed that width increments triggered a drop in some parameters of the foraging process: termites ate less and walked more on larger platforms than in narrow ones. The amount of, head-on encounters (collisions) decreased on larger platforms. At the microscopic scale, we found that collisions are key to inhibit the tendency of individuals to reverse their walking direction as well as to prevent termites from halting in foraging trails. Collisions also modulated termites' speed. Our findings indicate that termite traffic is a collective behaviour that emerges from interindividual interactions. The absence of traffic jams and, thence, its stability is a result of the coordinated (co-operative) movements resulting from inhibitory interactions.

key words: Traffic dynamic, Termites, Cooperation based on inhibition.

3.1 Introduction

Traffic flow formation is an exclusive phenomenon of societies. To understand traffic formation we need to analyse its two forces: physical (Kerner, 2004) and social (Helbing and Molnar, 1995). From physics, traffic results from the collective movement of the entities (animals, people, or cars) who need to coordinate their speeds and created coherent direction flows (Ball, 2004). The social component of traffic formation is based on the interdependence and eventual interindividual interactions between these. Construction of permanent roads or highways is expensive for any society (Burd et al., 2002; Bochynek et al., 2019), being usually constructed by central-place foragers as modern humans (Premo, 2015) and leaf-cutting ants (Bochynek et al., 2019). These costs are optimized when routes allow traffic dynamics that maximize the number of individuals passing per unit time (flow) (Burd et al., 2002). However, individuals are in their own self-interest, preferring an empty road (Tumer et al., 2008; Helbing and Molnar, 1995). Fundamentally, the survival of a society depends on the ability of individuals to deal with the constraints of sharing the road with others. For that reason, the traffic dynamics of society may reveal how its individuals resolve that conflict of interest.

Contrary to human societies' traffic, the flow forming by some social insects like ants or termites seems continuous, smooth, highly organized, and unbreakable. Termites are eusocial, they have an extreme condition of sociability where individuals behave as a "superorganism" (Wilson, 1992) almost-all sacrificing their own reproduction. However, how individuals collectively self-regulate to achieve such stable traffic is unknown. Here we tested the stability of termites' flow in order to search for the mechanisms behind their highly organized traffic. Cooperative interactions have been suggested as a key element in traffic dynamics (Helbing and Huberman, 1998). Cooperation is commonly associated with the act of helping others; however, in the traffic dynamics to cooperate means to coordinate or to work together. As individuals are constrained by their neighbors' movement, such coordination in trafficking particles can arise from unsuspected behaviours like competition (Helbing and Huberman, 1998) or the inhibition of free movements (Burd, 2000; Dussutour et al., 2004). Because cooperation seems to be essential for determining the pattern of traffic flow, interactions between termites who potentially lead to coordinated movements were central in this research.

The causes of traffic breakdown come from heterogeneity (Campanella et al., 2009). In living systems, in addition to the heterogeneity of their environment, there is an internal heterogeneity resulting from the anatomic and behavioral differences of individuals. For example, a taller individual can prefer to walk faster than a smaller one, resulting in a faster person will desire to overtake the slowest individuals ahead. This could lead to sudden changes in position performed by individuals avoiding collisions which, ultimately, could trigger local and momentary jams that percolate as a traffic breakdown. Besides internal heterogeneity, there is heterogeneity becoming from external conditions like climate, the design, the width, or the material covering the road's surface. The width of the road acts constraining the maximum flow supported (Smeed, 1967, 1968).

Here we studied the reasons for the stability of the traffic in termite foraging trails, inspecting the effects of external heterogeneity on macroscale parameters of the foraging process in these insects. Then we proceeded studying putative mechanisms for such stability, at the individual level. To do so, we forced *C. cyphergaster* termites to travel between the nest and the foraging arena on platforms of 7 different widths measuring at the colony level, their speed, the amount of food consumed per time interval, the distance travelled, and the amount of head-to-head collisions. Then we inspected, at the individual scale, how interindividual collisions would affect their traffic direction. *C. cyphergaster* societies share some traits with human civilization like the thousand of individuals involved in traffic formation, the central-place forager condition, and the formation of trails that admit individuals moving in opposite directions. Such features justifying the use of the foraging process of *C. cyphergaster* to study complex traffic-related phenomenon as a surrogate for human pedestrian traffic.

3.2 Methods

3.2.1 Sampling, Ethics Statement

We used as biological model *C. cyphergaster* (Blattaria: Isoptera: Termitidae: Nasutitermitinae) termites. 18 nests with no sign of damage were collected in the "Cerrado" Brazilian Biome in the Rural District of São José das Lajes, Municipality of Cordisburgo (S19°2', W44°15'), State of Minas Gerais, Southeastern Brazil. In total, we made two expeditions, the first from 17th to 19th June 2018; the second from 6th to 8th September 2018. The climate

of the study area corresponds to Cwa (humid Subtropical, with dry winter and hot summer) in the Köppen system (Alvares et al., 2013). O. DeSouza holds a permanent permit from IBAMA (The Brazilian Institute for the Environment and Renewable Natural Resources) to collect termites. Neither protected species were sampled nor genetical information was accessed.

3.2.2 Overall rationale

To test the stability of termites' traffic to external heterogeneity, we examined macroscale parameters of their foraging dynamics by exposing the colonies to different widths of foraging platforms. The platforms connected the nest to the foraging arena. Then, to inspect the mechanisms underlying such parameters, we focused on the microscopic scale, analyzing the effect of inter-individual interactions between focal termites.

3.2.3 Nest maintenance in laboratory conditions

Termitaria with no sign of damage were removed from the field, put into plastic bags, labeled, and taken to the lab. Once there, nests were placed in plastic boxes and kept in a rearing room with controlled temperature and humidity. The boxes were covered with a small pore voile fabric to permit the exchange of gases and prevent the entrance of undesired arthropods. The temperature at the rearing room was modulated to oscillate between ≈ 21 and $\approx 28^\circ\text{C}$. The low temperatures were during the day and the maximum at night. That temperature variation was induced to prevent the feeding of termites at night (see Chapter 2). The reverse cycle of temperature was complemented with a reverse photoperiod of 12:12 h D:L. Water was provided *ad libitum* for termites in water-filled test tubes closed by a piece of cotton. Tree bark lichens and filter paper were offered *ad libitum* as food. The food and water-tubes were changed every two days.

3.2.4 Foraging experiment setup and data collection

We used the natural foraging behaviour of termites to induce their passage on the platforms. Were tested 18 whole colonies using 7 different widths (1.5, 2.5, 5.0, 7.5, 10, 12.5, 15.0 cm) (fig. 3.1).

The whole colonies were exposed to a starvation period of three days before the experiment. Water *ad libitum* was offered for the colonies all the time, even during the starvation period. On the experiment day, we

connected the box containing the nest to the foraging box using the respective platform (fig. 3.1). The platforms were constructed using styrofoam (length = 40 cm, width = variable) and fixed on the boxes with silicone glue. We covered the ground of the foraging arena with a previously (one day before the experiment) heat-treated soil at 111°C for two hours and preserving inside the laboratory oven until used. In the foraging box, we offered for termites between 22 and 23 gr of wet lichen and tree bark, 4 test tubes of water, and ≈ 1.15 gr of filter paper cut into eight parts. The experimentation room was conditioned with halogen lamps covered with red cellophane paper. Before we moved the nest, the temperature of the experimentation room was adjusted to have the same conditions of the rearing room (usually 23°C or 24°C, the temperature at 7:00 h). During the experiment, we regulated the temperature between 23 and 25°C. The nest was moved in the dark to didn't break the 12:12 reversed light cycle.

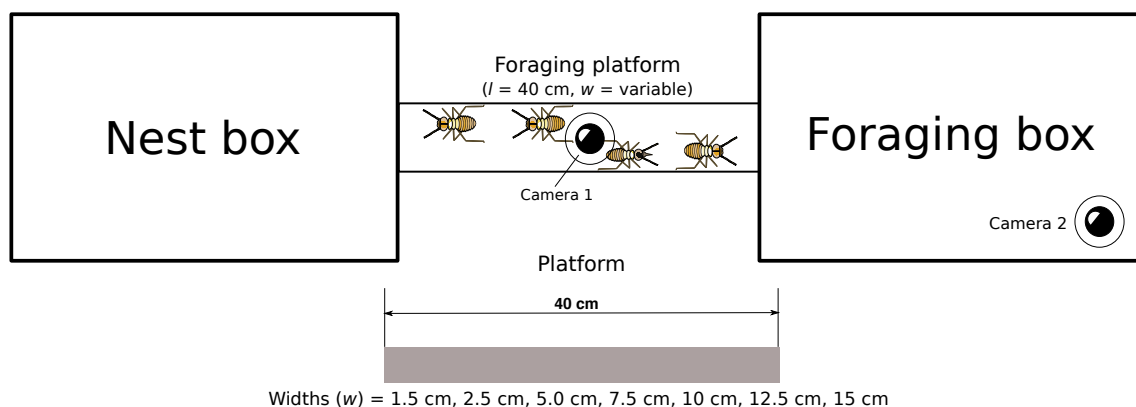


Figure 3.1: Foraging experiment setup top view. The nest box and the foraging box were connected with a platform of width variable.

We recorded the full foraging episode (≈ 10.2 h) of each termite colony that was assayed. For that, we placed above the center of the foraging platform a video camera remotely controlled. The video camera was activated at the first exit of the exploring group and turned off after all the individuals returned to the nest. We also registered the activity in the foraging box with a second video camera located above at a corner of the box (fig. 3.1). Simultaneously, we chose and visually followed focal termite workers and soldiers to register: the hour of observation, the distance travelled on the platform, time spent crossing that distance, and if the focal termite kept walking in the starting direction (recorded as 0) or if it reversed (recorded as 1). Additionally, we counted the number of head-on encounters (collisions) suffered by a focal termite when faced with a nestmate walking in the opposite direction. We considered both individuals outgoing (out-

bound direction) from the nest and ingoing (inbound direction). We manually tracked a total of 3700 *C. cyphergaster* termites, ≈ 200 individuals per nest. Pieces of filter paper of known weight were offered as foraging items, along with pieces of tree bark containing lichens and mosses. After foraging ended, we weighed the remains of the filter paper to estimate foraging efficiency.

3.2.5 Foraging efficiency

We measured foraging efficiency as the amount of food consumed (g) per nest volume (L) moving per hour (h). To calculate the efficiency first, we divided the volume of the nest between the hours of foraging. That calculation is a measure of flow, which means the volume in liters of the nest moving per hour to collect the food. Finally, we divided the grams of food consumed by the volume of the nest moving per hour ($g * (Lh)^{-1}$).

3.2.6 Testing statistical hypothesis

Macroscopic scale

To explore the effect of the platform width at the colony level we measured five parameters here defined globally as foraging process: (i) foraging efficiency, (ii) distance travelled on the foraging platform, (iii) the proportion of termites reversing walk direction, (iv) the proportion of workers arriving at the foraging box, and (v) the number of collisions faced by termites.

For all the response variables tested, we performed a Generalized Linear Modelling (GLM) and selected the best model using the second-order Akaike Information Criterion (AICc). We used the AICc difference between the candidate model and the 'best' model ($\Delta_i = AICc_i - AICc_{best}$) to rank the models. Models with $\Delta \leq 2$ were considered significantly supported. All the analyses were performed in R (R Core Team, 2020) using the MuMIn package (Barton and Barton, 2020).

We constructed a statistical model for the continuous response variables: foraging efficiency and distance travelled using a GLM with Gaussian error distribution. The variables were analyzed separately against the explanatory variable width of the foraging platform.

We proceeded to inspect if the head-on encounters (collisions) between termites were affected by the width of the platform. As a response variable, we used the mode of the number of collisions faced by focal individuals when moving along the platform in a given foraging bout. This

was done because count data follow a Poisson distribution (Crawley, 2012) were the mode (rather than the mean) represents the most frequent quantity. The platform width was used as the explanatory variable, and modelling proceeded under a GLM with Poisson error distribution. For the second model, the response variable consisted of the proportion of termites workers arriving at relative to the total number of workers who travelled in the outbound direction. As with the other response variables, we used the width of the platforms as the explanatory variable. Because we observed that termites changed the flow direction after faced a threshold of collisions, we included the number of collisions as a covariable in both independent models.

Microscopic scale

At the microscopic scale, we searched in the interindividual interactions (head-on encounters) the causes of the pattern observed at the macroscopic scale. From our observations during the experiments, we selected parameters related to traffic stability like the changes of direction, stopping in the middle of traffic, and the speed of focal termites to measure how interindividual interactions can affect them. For that, we inspected if collisions (explanatory variable) modified: (i) the probability of a termite to reverse its direction, (ii) the propensity of termites to halt, and (iii) the speed of focal termites.

As before, we performed GLM modelling and selected the best models using the AICc criterion and the $\Delta AICc$ to rank them. Only models with $\Delta \leq 2$ were considered with the help of the same statistical software.

Models included as explanatory variable the number of collisions faced by each focal individual when moving along the platform in a given foraging bout. Response variables were also recorded individually for each focal termite. To inspect the effect of collisions on the propensity of a termite to reverse its direction, data were subjected to logistic regression using GLM under binomial errors and logit link function. We aimed to determine whether the number of collisions faced by a given focal individual (x-var) would affect a binary response variable (y-var) describing whether this termite has reversed ($y = 1$) or not reversed ($y = 0$) its direction during a foraging bout.

To know if the head-on encounters (explanatory variable) can modulate the mean speed of focal termites, we performed a GLM under Gaussian error distribution.

Finally, we searched in the dynamic of collisions and speed during foraging additional evidence of the modulation of speed by the head-on encounters. To do this, we used the time elapsed from the beginning of foraging as the explanatory variable. For the case of collisions, we performed a GLM under Poisson error distribution while for speed we used the Gaussian error distribution. For all models, we included the caste of focal termites and the direction as explanatory covariables.

3.3 Results

3.3.1 Macroscopic scale

Modifications in the width of the platform (external heterogeneity) did not provoke jams or significant stopping points in termite traffic flow. Individuals from all *C. cyphergaster* termite nests here assayed found the food, fed, and returned successfully to the nest. However, the platform width modulated the efficiency, the mean distance travelled, the proportion of termites reversing the direction, and the collisions suffered. In the following subsections, we present the results at the colony (group) scale.

Foraging process

The foraging efficiency, measured as the food (filter paper) consumed relative to the flow of individuals in liters by hour ($g(hL)^{-1}$), decreased nonlinearly with the increments in the width of the platforms (tab. 3.1 (Efficiency), fig. 3.2). By each increment of 1 cm in the width of the platform, termite feeding drops $0.018 g(hL)^{-1}$.

Termites found a shortcut within the platform to travel between the boxes in narrow platforms. In consequence, the mean distance travelled by termites increased nonlinearly with enlargements in the width of the platform (tab. 3.1 (Distance), fig. 3.3). An increment of 1 cm in the width of the platform lengthened in 0.16 cm the mean distance travelled by termites between the nest and foraging box.

Table 3.1: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of the platform width on termites foraging efficiency (Efficiency) and the mean distance travelled (Distance). Foraging efficiency was measured as food consumed relative to the flow of nest in liters per hour ($g(hL)^{-1}$). Mean distance travelled refers to the distance walked by termites from the starting point on the platform (next to nest or foraging box) to the target (destiny box) or to a stopping point. Column headings: id = model identification, (Intrc) = model intercept, pltfr = width of the platform, pltfr² = quadratic width of the platform, df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

	id	(Intrc)	pltfr	pltfr ²	df	logLik	AICc	Δ	weight
Efficiency	1	0.45			2	0.9	3.5	0.00	0.50
	3	0.55		-0.001	3	2.0	4.7	1.27	0.26
	2	0.60	-0.017		3	1.7	5.3	1.82	0.20
	4	0.42	0.040	-0.003	4	2.2	8.6	5.13	0.04
Distance	1	36.54			2	-29.4	63.8	0.00	0.50
	2	35.35	0.154		3	-28.4	65.1	1.30	0.26
	3	35.91		0.008	3	-28.7	65.8	1.95	0.19
	4	34.26	0.566	-0.026	4	-27.9	68.3	4.47	0.05

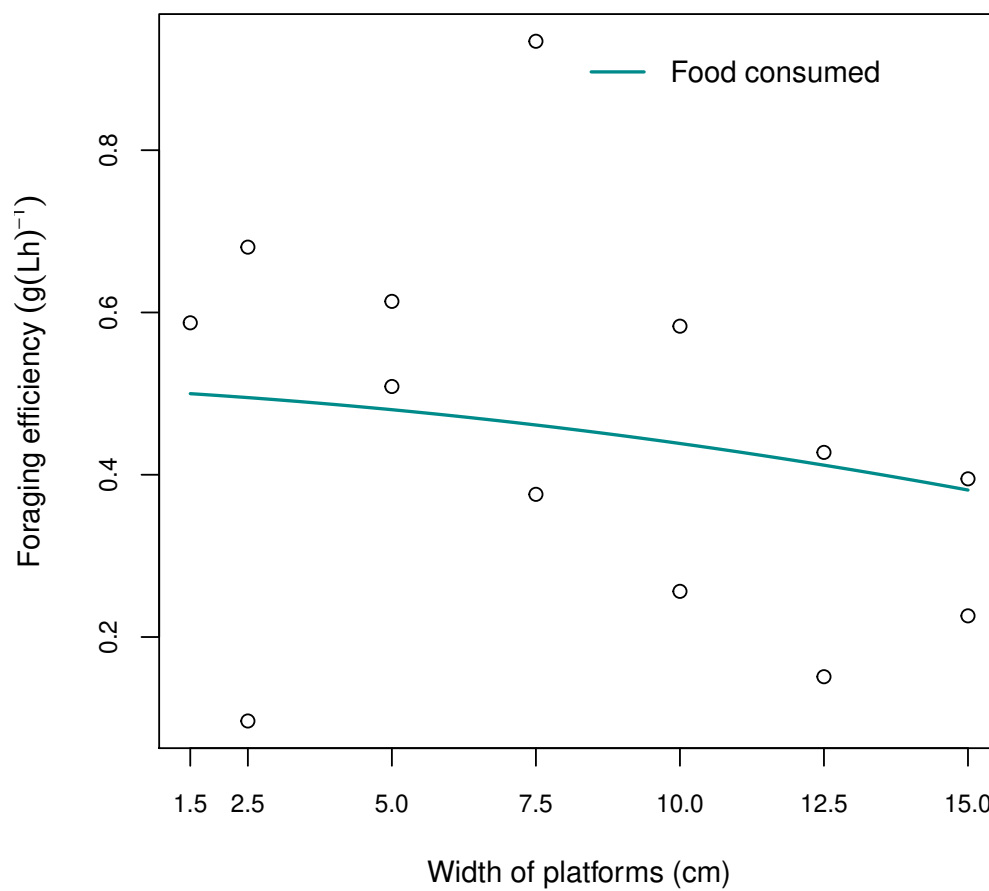


Figure 3.2: Termites foraging efficiency decreases nonlinearly with the increments in the width of the platforms. Foraging efficiency was calculated as the food (filter paper) consumed relative to the flow of the nest in liters per hour ($g(hL)^{-1}$). See table 3.1 (Efficiency) for statistical details.

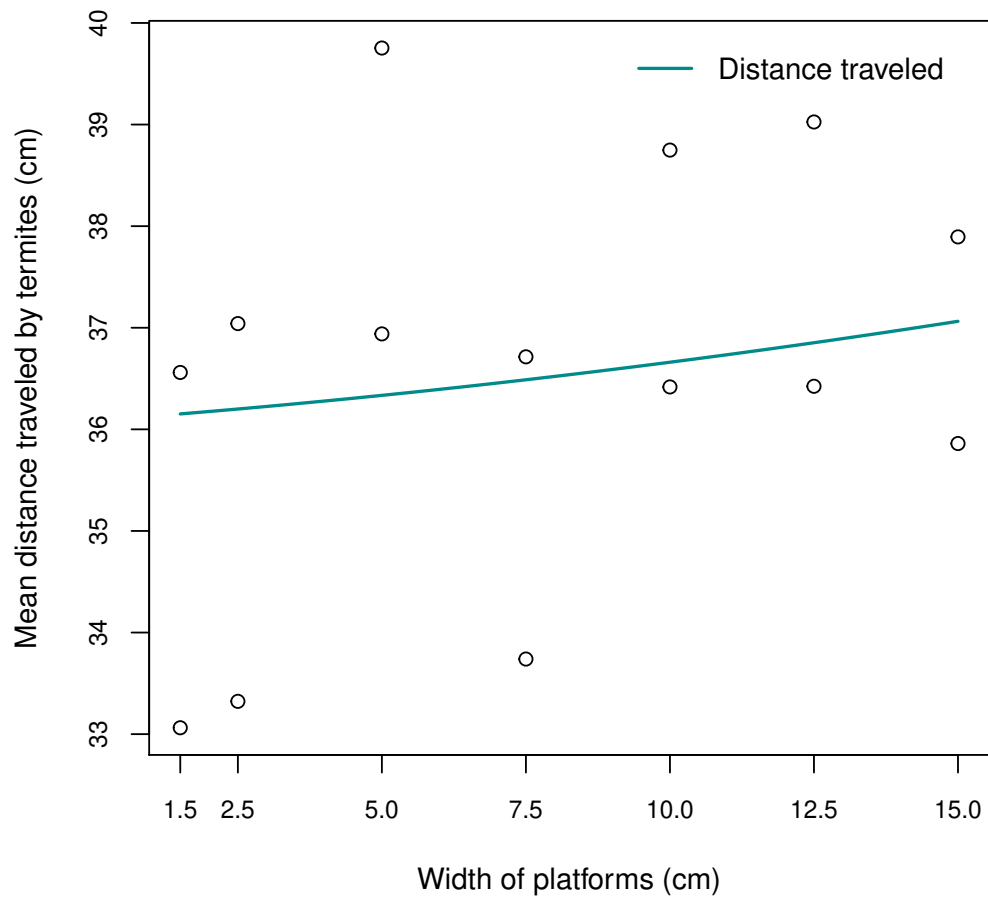


Figure 3.3: The mean distance travelled by termites increases nonlinearly with the enlargements in the width of the platform. See table 3.1 (Distance) for statistical details.

Collisions and changes in the flow direction performed by termites

The broader the platform, the smaller the number of head-on encounters (collisions) among foragers (tab. 3.2, fig. 3.4). The most frequent number of collisions per individual dropped from ≈ 8 in the broadest platform to ≈ 3 in the narrowest, along the whole foraging bout.

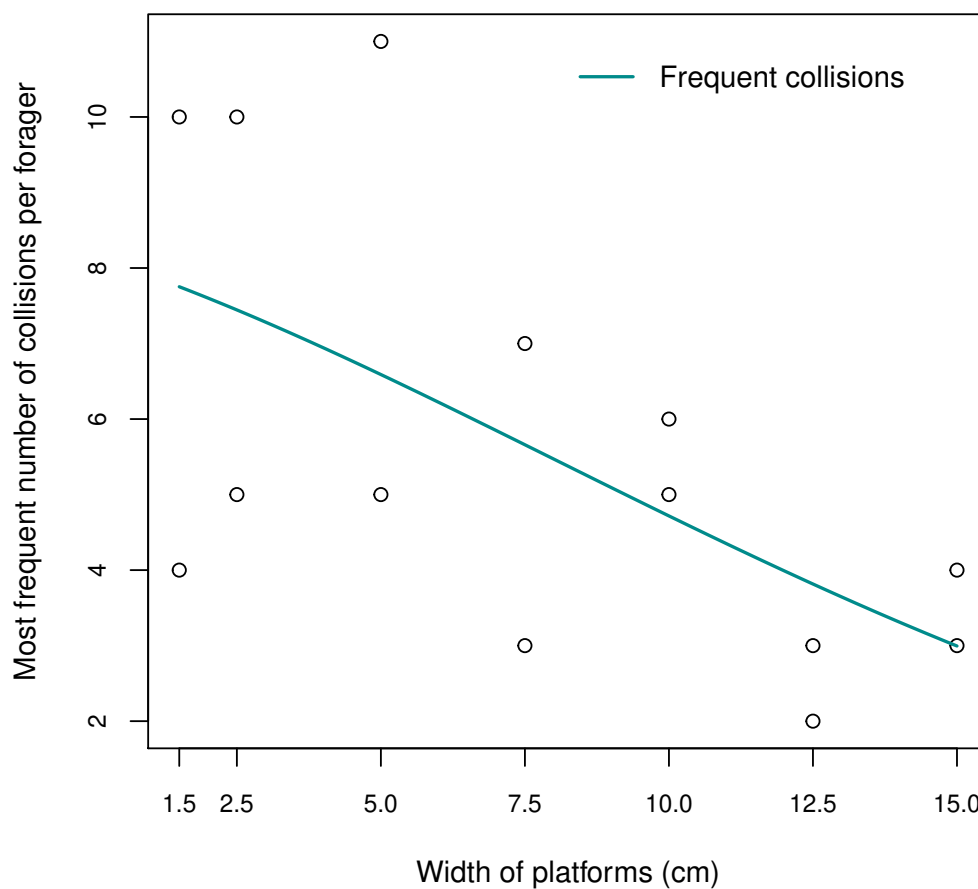


Figure 3.4: The most frequent number of collisions faced per forager along the whole foraging bout is a negative function of the platform width. See table 3.2 for statistical details.

Table 3.2: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of platform width on the most frequent number of collisions faced per foragers along the foraging bout. Collisions are the face to face encounter between termites moving in opposite directions. Column headings: id = model identification, (Intrc) = model intercept, pltfr = width of the platform, pltfr² = quadratic width of the platform, df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

id	(Intrc)	pltfr	pltfr ²	df	logLik	AICc	Δ	weight
3	2.03		-0.004	2	-29.8	64.7	0.00	0.47
2	2.19	-0.067		2	-30.0	65.0	0.34	0.40
4	2.04	-0.007	-0.004	3	-29.8	68.0	3.31	0.09

The broader of the platform, the higher the proportion of termites who changed the flow direction. For each increment of 1 cm in the width of platforms, ≈ 0.03 termites changed the movement orientation. However, the platform width did not fully explain the tendency of termites to change the traffic direction. Collisions also modulated termites' propensity to change traffic orientation. U-turns towards the nest were more commonly observed when individuals suffered fewer collisions. The loss of one collision triggered that ≈ 0.98 termites changed the flow direction. (tab. 3.3, fig. 3.5).

Table 3.3: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of platform width and interindividual collisions on the proportion of termites changing traffic direction. Column headings: id = model identification, (Intrc) = model intercept, pltfr = width of the platform, cllsF = more frequently number of collisions faced by foragers, df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

id	(Intrc)	pltfr	cllsF	df	logLik	AICc	Δ	weight
2	-0.54		-0.115	2	-67.52	140.1	0.00	0.67
4	-0.74	0.015	-0.099	3	-66.57	141.5	1.41	0.33
3	-1.51	0.046		2	-77.50	160.1	19.96	0.00

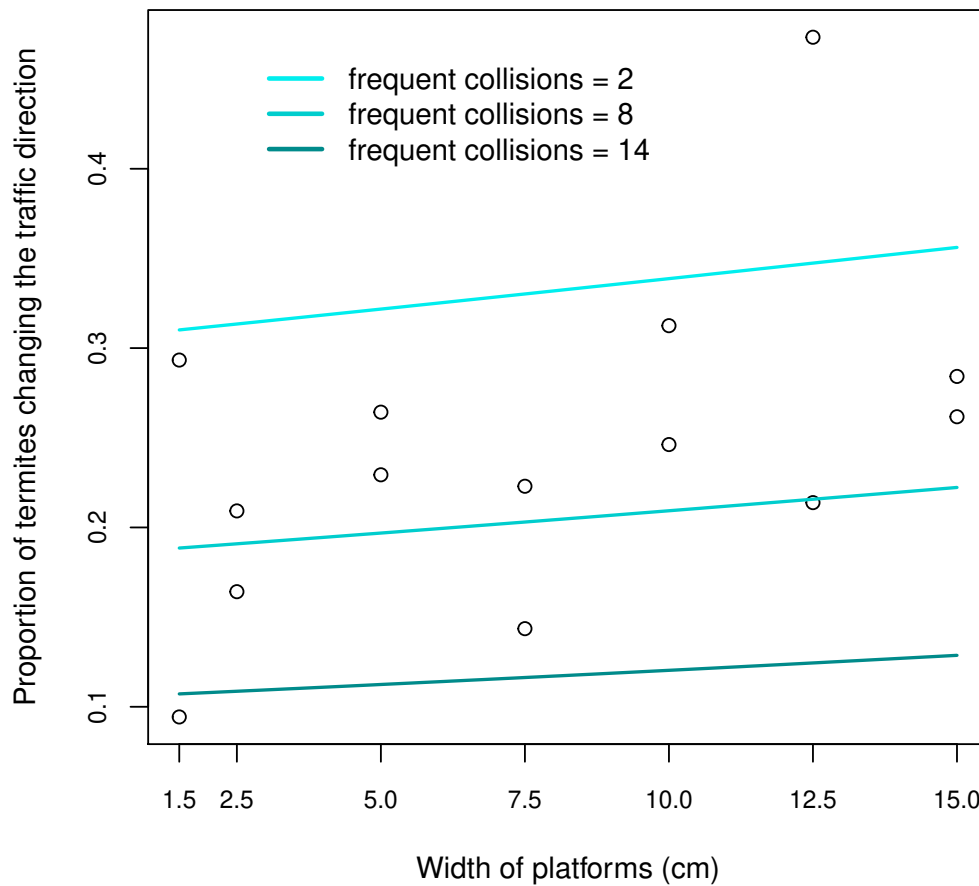


Figure 3.5: Termites changed their traffic direction more often as the width of the platform increased. Each enlargement of 1cm in platform width triggered that ≈ 0.03 termites modified their traffic direction. The propensity of termites to change their traffic direction decreased with the increments in the number of collisions they have faced. See table 3.2 for statistical details.

Both the width of the platform and the number of collisions experienced regulated the proportion of termite workers reaching the foraging box. The larger the width of the platform, the lower the proportion of workers arriving at the foraging box. This negative effect of platform width is more pronounced under less collisions (fig. 3.6, tab. 3.4).

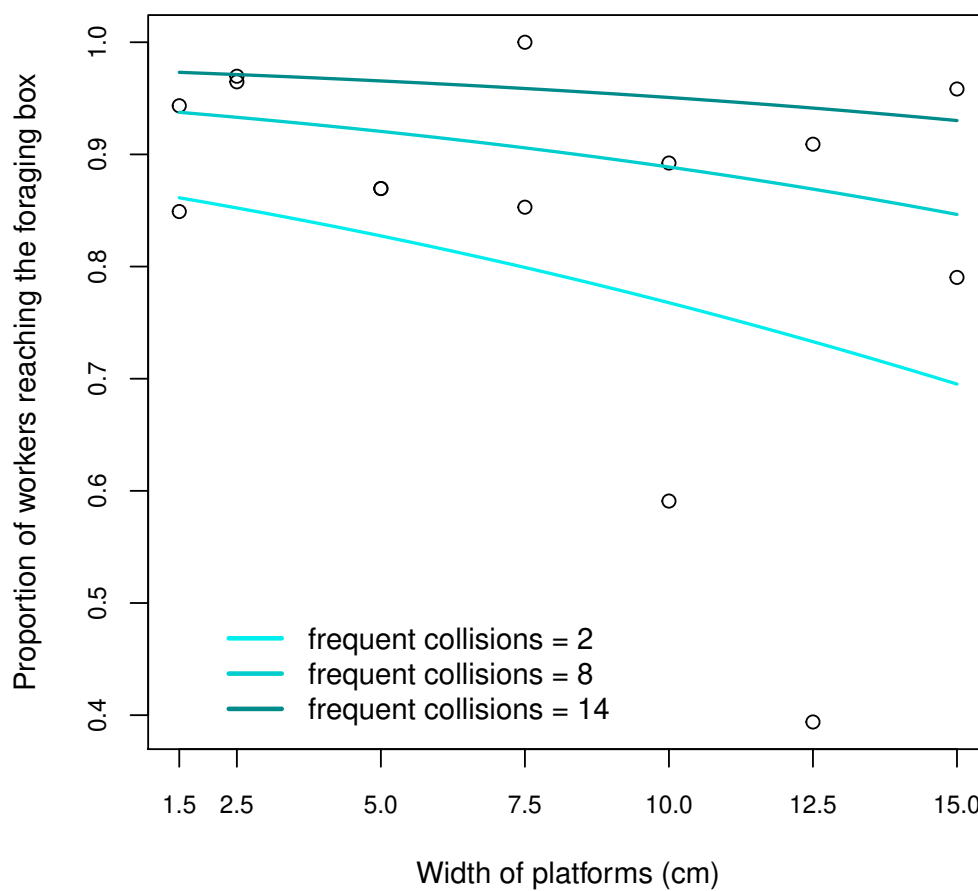


Figure 3.6: Termite workers arriving at the foraging box decreased with increments in the width of the platform. However, this effect was offset when termites experienced more collisions. See table 3.4 for statistical details.

Table 3.4: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of platform width and interindividual collisions on the proportion of termites arriving at the foraging box. Column headings: id = model identification, (Intrc) = model intercept, pltfr = width of the platform, cllsF = more frequent number collisions faced by foragers, df = degrees of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

id	(Intrc)	pltfr	cllsF	df	logLik	AICc	Δ	weight
4	1.64	-0.074	0.147	3	-57.53	123.5	0.00	0.69
3	2.76	-0.117		2	-60.40	125.9	2.44	0.20

3.3.2 Microscopic scale

In the previous subsection, we analyzed the effect of the width of the platform at colony level (macroscopic scale) on the termites' foraging. While in this subsection, we analyzed the termites' traffic dynamic at the level of inter-individual interactions. Then at this microscopic scale, the focus was interindividual collisions instead of the width of the platform. The goal of this analysis was to know why variations on platform width triggered costs on termites foraging process even when not causing traffic jams. The results are shown below.

Probability of changing traffic-flow direction

Collisions modulated the probability of termites to changed their traffic direction. Individuals tended to make less U-turns as they've faced more interindividual collisions (tab. 3.5, fig. 3.7, full results in Appx. I). In most cases, the covariables caste and direction also were included in the more likely statistical models. In general, termite soldiers displayed more propensity to change the movement direction than workers. Termites walking in the inbound route were more likely to change the traffic-flow direction than individuals moving in the outbound lane.

Table 3.5: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of collisions on the probability of termites reverse the traffic direction. Change in traffic-flow direction means that the focal termite eventually modified its route returning towards the starting point. Column headings: id = model identification, (Intrc) = model intercept, cllsn = number of face-face encounters (collisions) between termites moving in opposite directions, caste = caste of the focal termite (worker or soldier), drctn = movement orientation of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight. Full results in Appx. I

	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight
N01	4	0.58	-0.161	+		3	-119.1	244.3	0.00	0.39
	8	0.66	-0.142	+	+	4	-118.2	244.5	0.23	0.35
	3	0.35	-0.168			2	-121.0	246.1	1.83	0.16
	7	0.40	-0.152		+	3	-120.4	246.8	2.52	0.11
N05	4	1.05	-0.205	+	+	3	-131.0	268.1	0.00	0.56
	8	1.12	-0.200	+	+	4	-130.7	269.6	1.45	0.27
	3	0.73	-0.203			2	-133.6	271.2	3.10	0.12
N09	3	0.50	-0.199			2	-127.2	258.4	0.00	0.32
	7	0.57	-0.186		+	3	-126.4	258.9	0.52	0.24
	4	0.61	-0.191	+		3	-126.4	258.9	0.57	0.22
	8	0.71	-0.177	+	+	4	-125.5	259.2	0.85	0.21
	6	-0.39		+	+	3	-139.5	285.0	26.6	0.00
	7	0.10	-0.149		+	3	-126.6	259.3	0.00	0.53
N13	8	0.17	-0.146	+	+	4	-126.4	260.9	1.60	0.24
	3	0.32	-0.137			2	-128.8	261.7	2.38	0.16

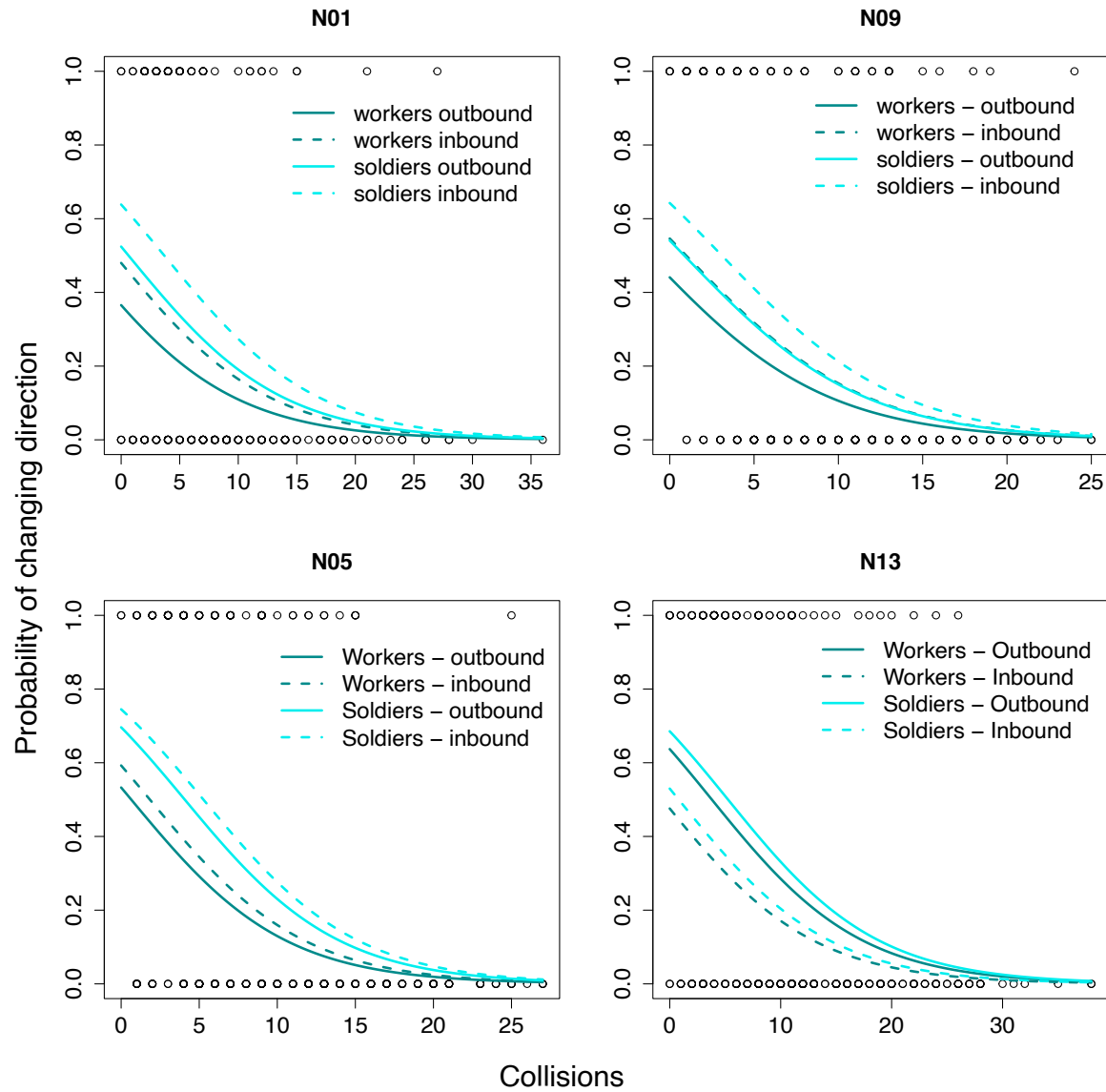


Figure 3.7: Termites had less propensity to change their initial traffic-flow direction as they faced more collisions. Termite soldiers were more likely to change the traffic-flow orientation than workers. Individuals moving in the inbound lane changed more frequently than individuals in the outbound route. For the results of all the nests see Appx. I

Halting propensity of termites

When walking along the platform, some termites tended to halt after facing collisions. Then, they either changed their behaviour or resumed walking. Behaviours happening after halting depended on the caste of the individual. Termite workers halted, contracted the body, did not make antennal contact with the nestmates around, and seemingly bitted the platform. Commonly workers remained halted for some seconds after which they continued moving in the initial direction. Termite soldiers meanwhile stopped at the lateral of the trail and assumed guard posture, facing outwards, with the longer axis of their body perpendicular to the traffic lane.

Collisions regulated termites' propensity to halt. With increments in the number of collisions termites were less prone to stop (tab. 4.2). Termite workers were less susceptible to halt than soldiers. Individuals moving in the outbound direction halted more frequently than the ones in the inbound lane (tab. 4.2, fig. 3.8).

Table 3.6: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of collisions on the termites' propensity to halt while walking in a foraging trail. Column headings: id = model identification, (Intrc) = model intercept, cllsn = number of head-on encounters (collisions) between termites moving in opposite directions, caste = caste of the focal termite (worker or soldier), drctn = direction of movement of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight. Full results in Appx. II

	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight	
N01	5	-3.33			+	2	-50.8	105.7	0.00	0.33	
	1	-2.71				1	-52.4	106.9	1.20	0.18	
	7	-3.16	-0.030			+	3	-50.6	107.3	1.66	0.14
	6	-3.21		+	+	3	-50.7	107.5	1.84	0.13	
	2	-2.59		+		2	-52.3	108.7	3.02	0.07	
N05	4	-1.47	-0.108	+		3	-49.4	104.9	0.00	0.43	
	8	-1.69	-0.123	+	+	4	-48.8	105.8	0.89	0.28	
	2	-2.37		+		2	-51.4	106.9	2.01	0.16	
	6	-2.55		+	+	3	-51.2	108.6	3.67	0.07	
N09	3	-2.46	-0.177			2	-26.7	57.5	0.00	0.24	
	4	-2.24	-0.148	+		3	-25.8	57.7	0.26	0.21	
	2	-3.24		+		2	-27.2	58.4	0.92	0.15	
	1	-3.76				1	-28.6	59.3	1.80	0.10	
	7	-2.44	-0.172			+	3	-26.7	59.5	2.03	0.09
	8	-2.21	-0.140	+	+	4	-25.8	59.8	2.26	0.08	
N13	2	-3.06		+		2	-24.5	53.0	0.00	0.49	
	4	-2.77	-0.031	+		3	-24.4	54.8	1.80	0.20	
	6	-3.06		+	+	3	-24.5	55.1	2.05	0.18	
	8	-2.80	-0.032	+	+	4	-24.4	56.9	3.84	0.07	

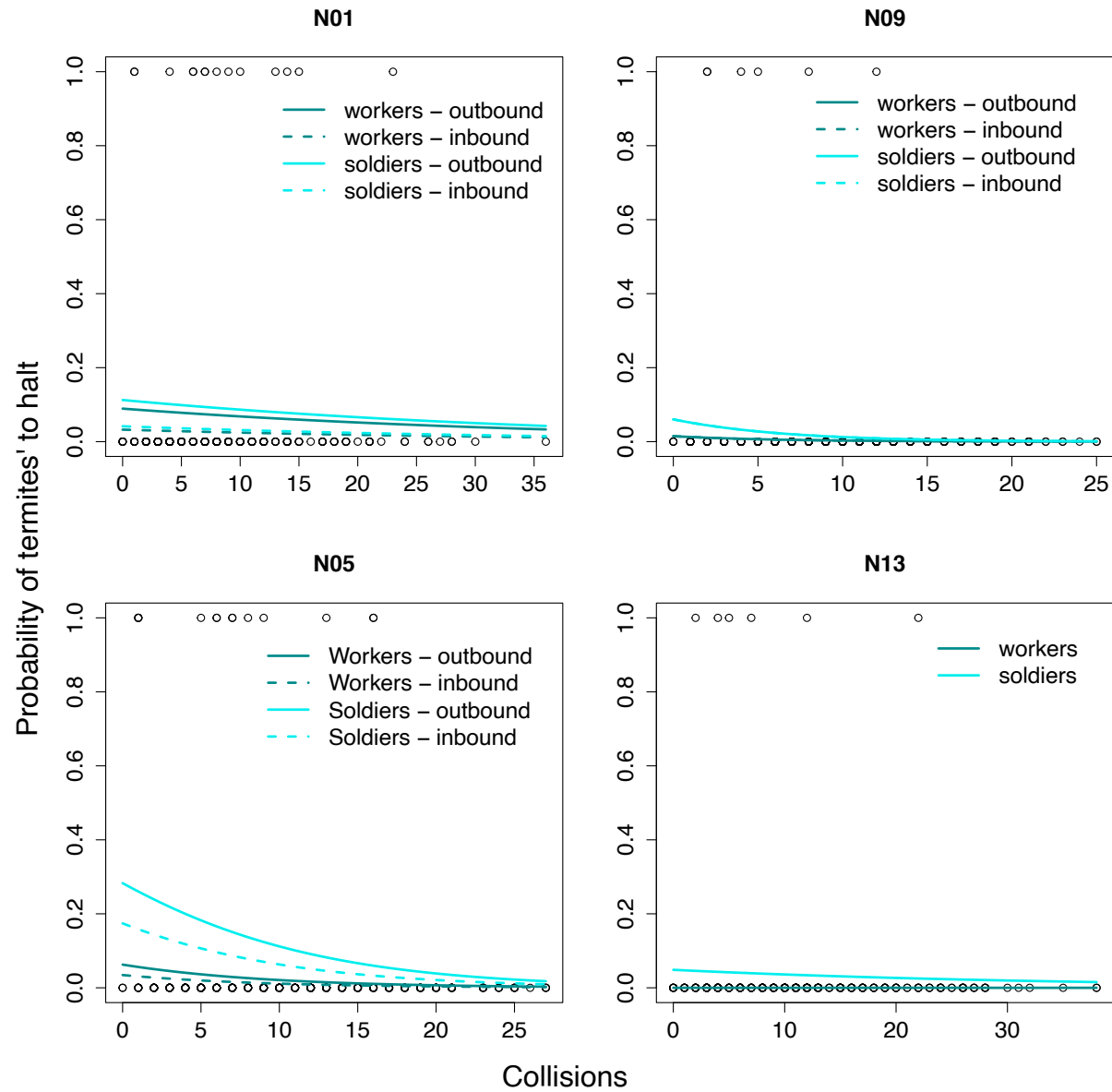


Figure 3.8: The probability of termites' halt decreased with the increments in the number of collisions. Termite workers were less susceptible to stop than soldiers. Individuals moving in the Outbound lane halted more frequently than individuals in the inbound route. For the results of all the nests see Appx. II.

Speed

Collisions also regulated how quickly termites walked on the platform. In most cases, the number of collisions with other nestmates triggered non-linear dynamics in the mean speed of focal termites (tab. 4.3, fig. 3.9). At low collisions (from 1 to ≈ 10) termites were stimulated to gain speed with a peak between 10 and ≈ 15 collisions. After that (> 15), termites became slower (fig. 3.9). Termite workers tended to develop speedy walks than soldiers. Individuals walking in the inbound route higher speed than termites in the outbound lane (fig. 3.9).

Table 3.7: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of collisions on termites' mean speed along the foraging platform. Column headings: id = model identification, (Intrc) = model intercept, cllsn = number of face-face encounters (collisions) between termites moving in opposite directions, cllsn² = quadratic form of collisions, caste = caste of the focal termite (worker or soldier), drctn = movement orientation of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight. Full results in Appx. III

	id	(Intrc)	cllsn	cllsn ²	caste	drctn	df	logLik	AICc	Δ	weight
	1	-0.14					2	-76.9	157.9	0.00	0.21
N01	7	-0.25	0.022	-7.8e-04			4	-75.3	158.8	0.87	0.14
	3	-0.17	0.003				3	-76.7	159.5	1.55	0.10
	5	-0.15		2.0e-05			3	-76.9	160.0	2.04	0.08
N05	6	-0.29	0.043	-0.001	+	+	6	-60.1	132.6	0.00	0.89
	8	-0.32	0.040	-0.001	+		5	-64.1	138.3	5.73	0.05
	16	-0.43	0.063	-2.5e-03	+	+	6	44.7	-77.2	0.00	0.36
	8	-0.43	0.060	-2.5e-03	+		5	43.3	-76.4	0.73	0.25
N09	5	-0.41	0.065	-2.6e-03		+	5	43.3	-76.4	0.76	0.25
	7	-0.42	0.062	-2.5e-03			4	41.7	-75.2	2.00	0.13
	4	-0.22	0.006		+		4	26.0	-43.9	33.30	0.00
	15	-0.07	0.026	-8.7e-04		+	5	-106.2	222.6	0.00	0.37
N13	6	-0.09	0.026	-8.7e-04	+	+	6	-105.6	223.5	0.93	0.24
	9	0.06				+	3	-109.8	225.6	3.07	0.08

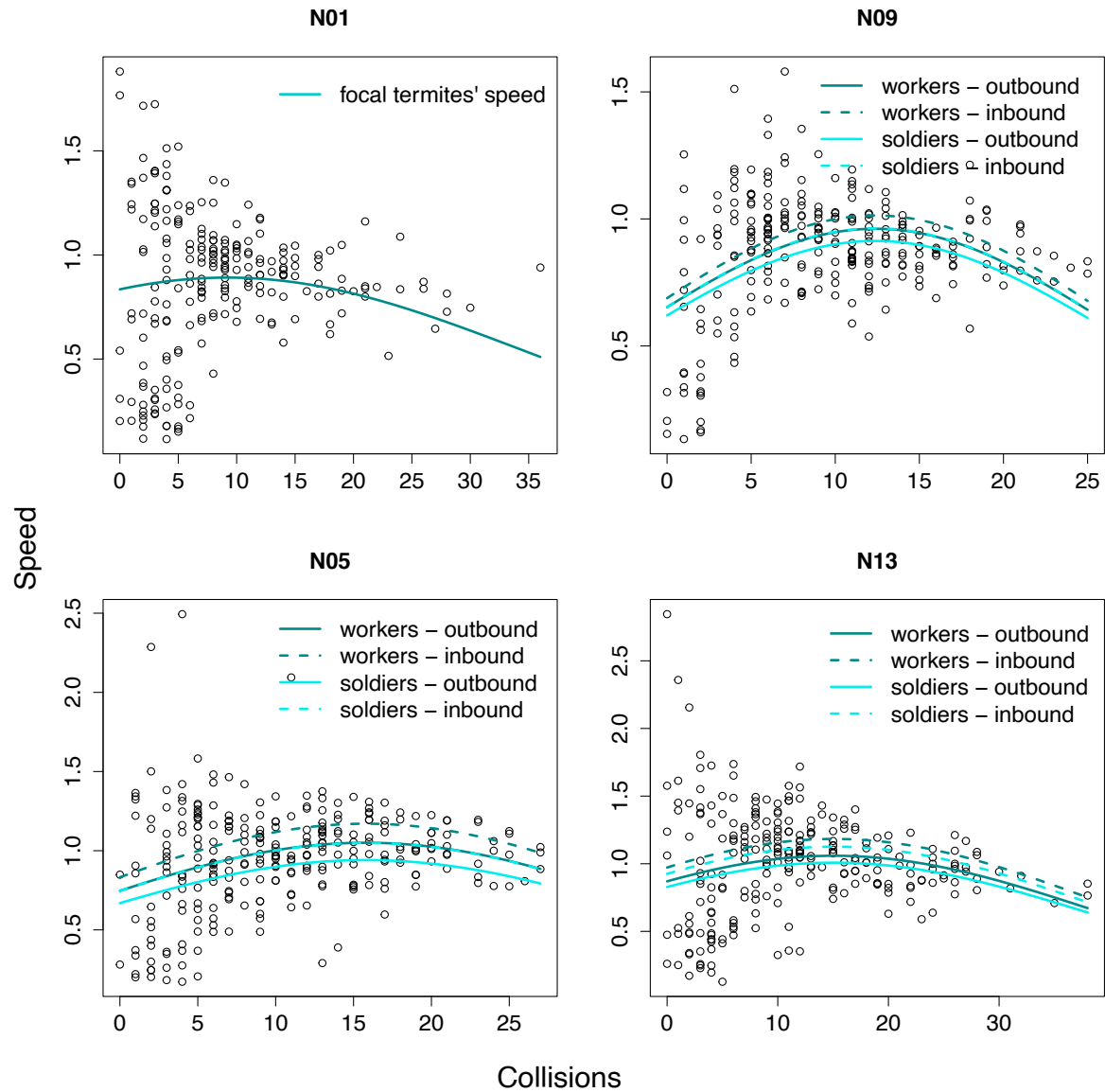


Figure 3.9: Termites modulated their speed in a function of the number of collisions with nestmates. Under lower collisions, termites were stimulated to increase their speed. Under higher collisions, the mean speed of individuals decreased. Termite workers frequently moved faster than soldiers. The inbound lane favored higher speeds. For the results of all the nests see Appx. III.

Speed and collisions dynamics along the foraging episode

Speed and collisions dynamics along the foraging episode showed a mirrored (inverse) pattern. There is a quadratic and negative correlation between the time elapsed from the starting of foraging and the speed of focal termites (tab. 4.4 - Speed). The minimum peak of velocity appeared close to the middle of the foraging episode. Individuals were faster in both the starting and final parts of foraging (fig. 3.10 - speed). On the other hand, collisions and the time elapsed from the beginning of foraging had a quadratic and positive correlation (tab. 4.4 - Collisions). The peak, in this case of maximum contacts, occurred close to the middle of the foraging episode while minimal collisions at the starting and endpoints (fig. 3.10 - Collisions). Individuals in the outbound direction faced more collisions and were slower than termites travelled in the inbound lane who dealt with few contacts. Termite workers were faster and faced more collisions than soldiers (fig. 3.10).

Table 3.8: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the dynamic of collisions and speed during the foraging episode. The time was measured as the hours elapsed from the starting of the foraging. Column headings: id = model identification, (Intrc) = model intercept, time = time in hours elapsed from the beginning of foraging episode, time² = quadratic form of the time elapsed, caste = caste of the focal termite (worker or soldier), drctn = movement orientation of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight. Full results in Appx. IV

	id	(Intrc)	time	time ²	caste	drctn	df	logLik	AICc	Δ	weight	
Speed	N01	13	-0.06	-0.116	0.015			4	-60.9	129.9	0.00	0.53
		14	-0.07	-0.116	0.015	+		5	-60.8	131.9	1.96	0.20
		15	-0.06	-0.116	0.015		+	5	-60.9	132.0	2.08	0.19
	N05	12	-0.11		0.002	+	+	5	-68.9	148.1	0.00	0.22
		16	-0.02	-0.049	0.007	+	+	6	-68.1	148.5	0.39	0.18
		8	-0.12	0.013		+	+	5	-69.5	149.2	1.15	0.12
		10	-0.14		0.002	+		4	-70.6	149.2	1.18	0.12
		14	-0.05	-0.050	0.007	+		5	-69.7	149.5	1.45	0.10
		4	-0.07			+	+	4	-70.7	149.6	1.54	0.10
		6	-0.16	0.013		+		4	-71.1	150.4	2.33	0.07
	N09	14	-0.11	-0.038	0.004	+		5	25.7	-41.1	0.00	0.24
		2	-0.17			+		3	23.5	-40.9	0.19	0.22
		10	-0.19		0.001	+		4	24.0	-39.8	1.26	0.13
		6	-0.19	0.003		+		4	23.6	-39.1	2.00	0.09
		16	-0.12	-0.038	0.004	+	+	6	25.7	-39.0	2.09	0.09
N13	8	-0.27	0.053		+	+	5	-65.6	141.4	0.00	0.55	
	16	-0.31	0.073	-0.002	+	+	6	-65.2	142.7	1.32	0.28	
	7	-0.22	0.051			+	4	-68.3	144.8	3.40	0.10	
Collisions	N01	16	1.44	0.130	-0.012	+	+	5	-818.3	1646.9	0.00	1.00
		8	1.61	0.015		+	+	4	-825.5	1659.2	12.38	0.00
	N05	16	1.41	0.328	-0.030	+	+	5	-1045.1	2100.4	0.00	1.00
		15	1.50	0.326	-0.030		+	4	-1055.5	2119.2	18.82	0.00
	N09	16	1.93	0.050	-0.007	+	+	5	-901.0	1812.3	0.00	0.64
		12	2.03		-0.003	+	+	4	-902.7	1813.6	1.34	0.33
		8	2.05	-0.023		+	+	4	-905.0	1818.1	5.79	0.04
	N13	16	2.06	0.132	-0.015	+	+	5	-1087.8	2185.8	0.00	1.00
		12	2.31		-0.004	+	+	4	-1109.4	2227.1	41.26	0.00

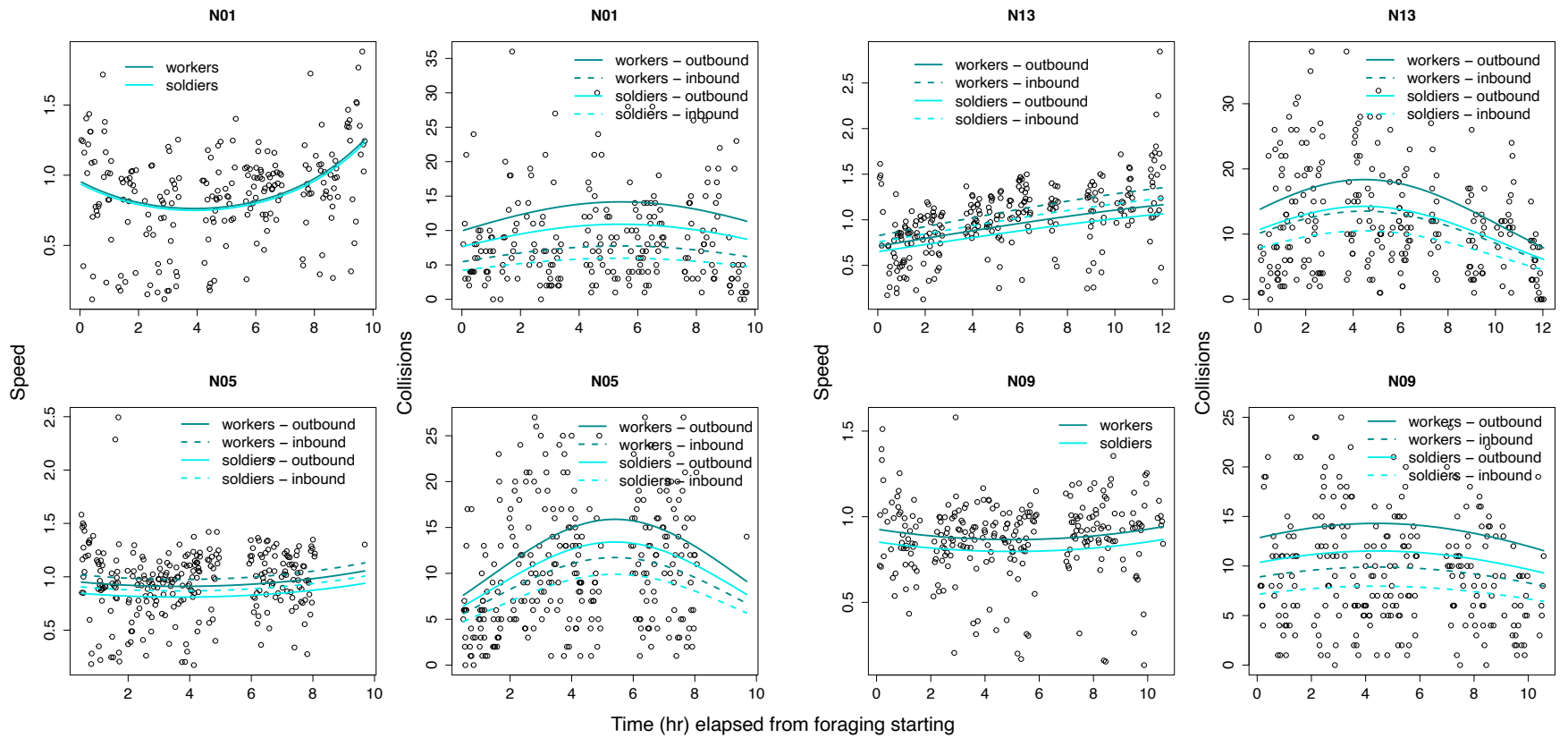


Figure 3.10: The dynamic of speed and collisions during the foraging behaved like a mirror with inverse and complementary patterns. There is a quadratic and negative correlation between speed and the time elapsed from the beginning of foraging. The minimum peak of velocity is close to the middle of the episode. On the other hand, collisions and the time elapsed correlated quadratic and positively. The maximum of collisions occurred close to the midpoint of foraging. For the results of all the nests see Appx. IV.

3.4 Discussion

3.4.1 Macroscopic scale

Termites trails - unlike human pedestrian or vehicular traffic - seem immune to external variability as a trigger of traffic jams. From the analysis of the 147.87 hours of the traffic of 3700 individuals from 18 independent nests, we showed that the width of the platform (ranging from 1.5 cm to 15 cm) did not trigger traffic jams in termite trails. External variability, however, was a significant modulator of the foraging process as a whole. The larger the width of the platform, the lower the foraging efficiency of termites, that is the amount of food they gathered per time (fig. 3.2, tab. 3.1). Our results indicate that this drop in the foraging efficiency resulted from at least two different processes: (i) the formation of alternative trails by strayed foragers (ii) the low rate of head-on encounters (collisions) between foragers moving in the opposite direction.

In wider platforms, termites had more space to create more optional trails (fig. 3.11) some of them being longer than others. This would imply that part of the foraging party would walk longer, thence the overall increment in distance travelled (fig. 3.3) and the overall reduction of efficiency in wider platforms (fig. 3.2). Interestingly, this phenomenon also happens in human pedestrians where the number of lanes rise linearly with the width of the walkway at maximum flow conditions (Helbing and Molnar, 1995).

Further, our findings also point out head-on encounters as modulators of termites' foraging process. Head-on encounters (collisions hereafter) are less frequent in wider as opposed to narrower platforms (fig. 3.4, tab. 3.2). Some authors propose that head-on encounters have a significant role in information transfer (Couzin and Franks, 2003; Cibils-Martina et al., 2017).

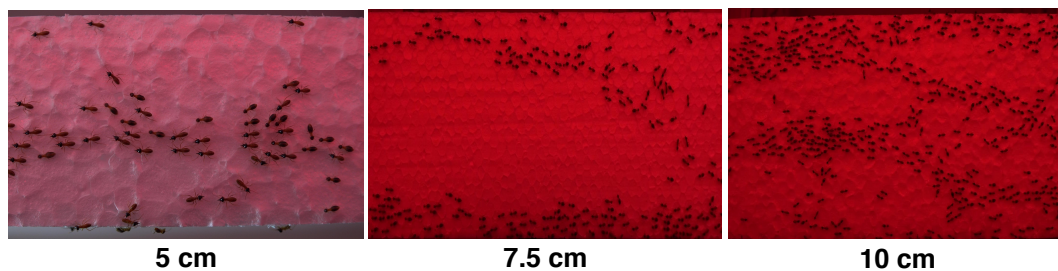


Figure 3.11: The number of alternative trails in termites' traffic scaling with the width of platforms. The photos refer to the dynamic of trails after 50 min of the beginning of foraging for the platform widths: 5 cm, 7.5 cm, 10 cm.

The simplest of this information would be that that route is under current use. That is, while trail pheromones inform that a route was once established in a given place, collisions would inform that the route is currently under use by the colony. A somewhat more complex hypothesis would sustain that these collisions could facilitate outgoing individuals to access the type and quality of food through the exchange of odor molecules present on the antenna and mouthparts of ingoing foragers. Accessing food information could have encouraged the outbound termites to continue in the same direction reducing the proportion of returning individuals. We tested this possibility for termite workers, who are responsible for collecting and transport the food into the nest. Our data strongly indicate the role of collisions to stimulate workers to reach the foraging box (fig. 3.6, tab. 3.4). In brief, collisions seem to provoke a domino effect: wider platforms lead to in lower density of individuals which, in turn, leads to less frequent collisions in wider as opposed to narrow platforms (fig. 3.4). In such a scenario, individuals become more susceptible to change the traffic direction (fig. 3.5), and that particularly true for workers heading to the foraging box (fig. 3.6). With fewer workers reaching the foraging box, less food is taken to the nest, scaling to the pattern of low foraging efficiency in the colonies with the increments in the platform width (fig. 3.2). Collisions have already been shown to improve foraging efficiency in ant colonies

(Bouchebti et al., 2015; Poissonnier et al., 2019). Interestingly, in nature, our focal species tend to form foraging trails that show similar width (≈ 2.4 cm, Fig. 12) with that of the narrow platforms (1.5 and 2.5 cm, fig. 3.12) here tested and shown to provide more efficient foraging.



Figure 3.12: Natural width of *C. cyphergaster* trails' observed in the field. Termites' trails in this species are narrow ($\approx 2.4\text{cm}$).

3.4.2 Microscopic scale

At the level of interindividual interactions (microscopic scale), our data support that a behavioral inhibition-base cooperation (in the sense of co-working, co-ordinate) prevents the termites' traffic from break-down.

Collisions inhibit the change of traffic direction and the tendency to stop

Validating the pattern found at the macroscopic scale (that is, patterns at group level), when a given individual faced more collisions it tended to not change its traffic direction (fig. 3.7, tab. 3.5). That is, head-on encounters seem to function as inhibitors of spontaneous movement to change direction, forcing alignment. This pattern was strongly consistent across the 18 nests tested (Appx. I). Inbound termites - mainly soldiers - were more

likely to change the flow orientation than outbound individuals (fig. 3.7, tab. 3.5); again indicating the role of collisions in information transfer.

Termite soldiers were more susceptible to change the traffic direction (fig. 3.7, tab. 3.5) regardless of their original direction. This finding seems suited to the soldiers' roles in termites' foraging: (i) scouts doing field reconnaissance and, (ii) nestmates' defenders.

Foraging in *C. cyphergaster* starts with the outgoing of an exploring group largely composed of soldiers. At this phase, soldiers walking slowly in a zig-zag pattern. At this point, soldiers exhibit a strong propensity to return to the nest, so that individuals in the front line are constantly replaced. Finally, when the exploring group finds food, individuals start an intensive return. We hypothesize that soldiers are primarily responsible for information transfer at this first phase of foraging in this termite species. Actually, our preliminary data suggest that the head-on encounters between outbound workers and inbound soldiers (102) are more frequent than workers(out)-workers(in) (70) contacts during the first hour of foraging. Interestingly, the same bias does not seem to happen for encounters between inbound workers and outbound soldiers (11) as compared to workers(in)-workers(out) (15) head-on encounters for the same period. Therefore, this massive return of the scout soldiers first finding food must enhance collisions and have a positive effect on recruiting workers to forage, a function traditionally associated with pheromone-trail deposition (Traniello, 1982; Hall and Traniello, 1985).

Soldiers as the specialized caste for termitarium defense seem to be naturally restless (Eisner et al., 1976; Deligne et al., 1981). In particular, for open foragers like *C. cyphergaster* highest mobility of soldiers should mean more chance to detect potential dangers as well as a quick dispersion of alerts. Earlier, Oster and Wilson (1978) suggested that soldiers improve benefits in foraging tasks as they defend against predators in the foraging

trail. Termite soldiers exploring, locating, and selecting the food source is largely known in many species of Nasutitermitinae subfamily (Traniello, 1981; Hafig et al., 2015; Almeida et al., 2016), here we report the same pattern for *C. cyphergaster*. In addition, here we report a new role for soldiers: to contribute, via collisions with outbound workers, to the coordination of the foraging trip in its initial phase.

Further, the inhibitory effect of collisions seems to be the base of coordination needed for the emergency of bidirectional flow in termite trails of *C. cyphergaster*. We found support for this idea in the postural adjustment of termites after collisions. We observed that after a head-on encounter, termites rotate the body away from the collider (fig. 3.13). This maneuver promotes a re-alignment of the focal termite's body with the termite's body in front of it. This forces the focal termite to return to its original direction, enhancing cooperative movement between the individuals traveling in the same lane and preserving the trail organization. As a consequence, the bidirectional flow of *C. cyphergaster* emerges when this simple process is replicated by each member of the foraging party.

Our findings also allow explaining how does foraging terminate despite the fact that, after many hours of foraging, stronger pheromone trails could have formed. As foragers start to satiate, they should tend to resume foraging less frequently. As a result, the foraging party would have less members and thence less collisions. Less collisions imply more U-turns of outgoers waning the foraging party up to its complete cessation.

The importance of collisions to movement is also evidenced by the fact that they prevented individuals to halt in trails. The probability of termites to halt decreased with the increments in the number of collisions they have faced (fig. 3.8, tab. 4.2). This indicates that short-time interactions like the head-on encounters are crucial for termites movement and traffic organization. Short-time interactions have been associated with traffic improvement

in ants (Poissonnier et al., 2019). Our hypothesis on information transfer could also explain why collisions prevent individuals from stopping. However, an alternative non-excluding hypothesis is that the simple interaction by itself may stimulate individuals to don't stop. According to social facilitation theory, individual performance improves in the presence of an audience or co-working individuals (Zajonc, 1965). Miramontes and DeSouza (1996) demonstrated that starving termites in Petri-dishes without food or water survive more when in the presence of nestmates than alone, even in the case of poisoned individuals (DeSouza et al., 2001).

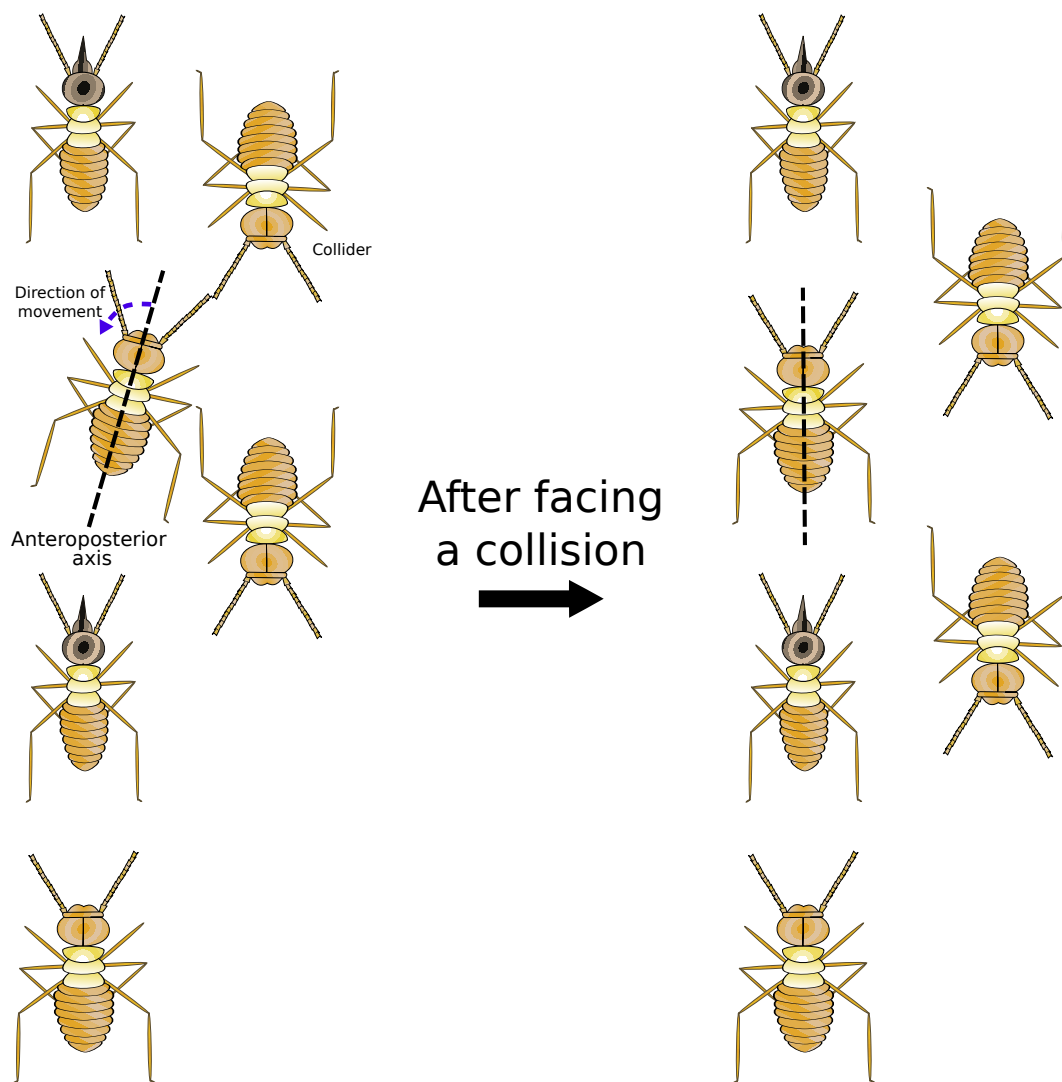


Figure 3.13: Behavioral observations on collisions triggering posture alignment in termites.

Collisions regulate the mean speed

Traffic theory postulates that the mean speed of particles (like vehicles or pedestrians) declines as density (particles per area) increases (Castillo and Benítez, 1995). That relation is central since it can determine the probability of traffic-breakdown. However, empirical studies show that the theoretical principle of the speed-density relationship doesn't apply to the traffic of some ants' species. In contrast, for some ants, the mean speed is constant when density rises (John et al., 2009; Wang and Song, 2016). Besides density, the head-on encounters also modulate the mean speed of individuals in traffic dynamics. Each collision in ants implies a time delay for stopping and exchange antennal contact, triggering loss in speed (Burd and Aranwela, 2003; Gravish et al., 2015). We also analyzed the relation between collisions and speed in foraging termites. However, our results show that in most nests collisions modulate nonlinearly the mean speed of termites: as collisions are enhanced, speed increases to a peak and reduces thereafter (fig. 3.9, tab. 4.3). That is to say, there is an optimal number of collisions which allow faster speed. This could be simply explained by the act of two opposing forces: the coordinating effect of collisions on movement along with the inevitable delay imposed by them. On one hand, collisions stimulate termites to stay on their lane (fig. 3.13) coordinating traffic and favouring flow. On the other hand, collisions and consequential returning to the original lane imply in some delay. Under low collisions, the balance between these forces is positive, but under a higher number of collisions, micro-delays accumulate to the point of impairing speed. These increments in delays will be particularly relevant if the number of foragers increases as time elapses and, with that, the density of the foraging party. We suspect the importance of density in the speed pattern found. Further analyses are

needed to uncover completely the relationship between collisions, density, and speed reported here.

On the other hand, the inverse pattern between collisions and speed reveals (tab. 4.4, fig. 3.10) that there is a coordination of the individual speeds in response to the head-on contacts. Collisions seem to act as an inhibitory agent of the free or preferred speed (speed of the individuals when collisions are zero). We hypothesize that by each collision, termites adjust their speed to the speed of their neighbors. By matching the speed provokes that termites move toward the center of mass of the trail, which could create cohesion between termites moving in the same lane resulting in organized bidirectional trails. Also, the peak of collisions is in the middle of the foraging episode (fig. 3.10), the point at which a balance between outbound and inbound foragers is expected.

All our data on the microscopic scale of termites' traffic suggest collisions as the primary factor to force cooperation necessary for a bidirectional flow. Far from avoiding collisions - despite their potential cost of reducing speed - termites seem to actively search for head-on encounters, particularly outgoing workers (fig. 3.10 - collisions). This can be explained by the need of these individuals to gather information to locate, collect, and transport the food to the nest. The soft body of termites, mainly of workers, as well as the incapacity of termites to anticipate interactions (they are blind), can also explain why termites don't avoid collisions. The elasticity of termites is the cause by which the head-on encounters don't damage their body, different from vehicles. The ability to anticipate interactions leads humans to avoid collision (Helbing, 1992). That anticipation is a cause by which individuals perform abrupt changes in direction and speed, increasing the probability of flow-breakdown (Helbing, 1992). In contrast, termites - blind insects - cannot anticipate interactions. The physical simplicity of termites and their high propensity to interact make it possible that these

insects individually sacrifice walk at their preferred speed to adjust to collective motion. This process seems individually sub-optimal; however, our data show that it creates co-working (cooperation) and is the key to prevent traffic jams.

3.5 Concluding remarks

Different from human societies, termites' traffic seems smooth and perfectly organized. To know the cause by which termites trails are resistant to jams bring the possibility to apply these principles to prevent this common and costly problem of cities. At the macroscopic level, we found that: (i) termite traffic doesn't form a jamming phase in response to external heterogeneity, (ii) external heterogeneity impact the foraging efficiency of termites. Our results at the microscopic level show that: (i) collisions inhibit the change of flow direction and the halting behaviour, (ii) the head-on contacts regulate the mean speed. In brief, our results support that termites prevent jams because they have an inhibition-base cooperation mechanism.

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3.7 Author contributions

Conceived and designed the experiments: JC, ODS. Performed the experiments: JC. Statistical modelling and analyses: JC, ODS. Biological interpretation of the models: JC, ODS. Contributed reagents/materials/analysis tools: ODS, JC. Wrote the paper: JC, ODS.

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Appendix

4.1 Appendix I: probability of change the traffic-flow direction

4.1.1 Statistical models

Table 4.1: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of collisions on the probability of termites reverse the traffic direction. Change in traffic-flow direction means that the focal termite eventually modified its route returning towards the starting point. Column headings: id = model identification, (Intrc) = model intercept, cllsn = number of face-face encounters (collisions) between termites moving in opposite directions, caste = caste of the focal termite (worker or soldier), drctn = movement orientation of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight
N01	4	0.58	-0.161	+		3	-119.1	244.3	0.00	0.39
	8	0.66	-0.142	+	+	4	-118.2	244.5	0.23	0.35
	3	0.35	-0.168			2	-121.0	246.1	1.83	0.16
	7	0.40	-0.152		+	3	-120.4	246.8	2.52	0.11
N02	3	-1.40	-0.093			2	-64.0	132.1	0.00	0.34
	4	-1.26	-0.086	+		3	-63.5	133.2	1.05	0.20
	7	-1.36	-0.092		+	3	-64.0	134.1	1.98	0.12
	1	-2.26				1	-66.2	134.5	2.39	0.10
N03	8	0.11	-0.059	+	+	4	-128.1	264.3	0.00	0.88
	4	-0.20	-0.067	+		3	-132.0	270.1	5.73	0.05
N04	8	2.51	-0.357	+	+	4	-89.5	187.2	0.00	0.99
	7	1.90	-0.343		+	3	-95.0	196.2	8.96	0.01
N05	4	1.05	-0.205	+	+	3	-131.0	268.1	0.00	0.56
	8	1.12	-0.200	+	+	4	-130.7	269.6	1.45	0.27
	3	0.73	-0.203			2	-133.6	271.2	3.10	0.12
N06	4	1.88	-0.228	+		3	-40.2	86.7	0.00	0.48
	8	1.70	-0.234	+	+	4	-39.8	88.0	1.32	0.25
	3	1.47	-0.229			2	-42.4	88.8	2.13	0.17
N07	8	0.44	-0.182	+	+	4	-65.4	138.9	0.00	0.48
	7	0.19	-0.189		+	3	-66.5	139.1	0.17	0.45
	3	0.07	-0.228			2	-70.0	144.1	5.18	0.04
	3	0.09	-0.16			2	-68.0	140.2	0.00	0.50

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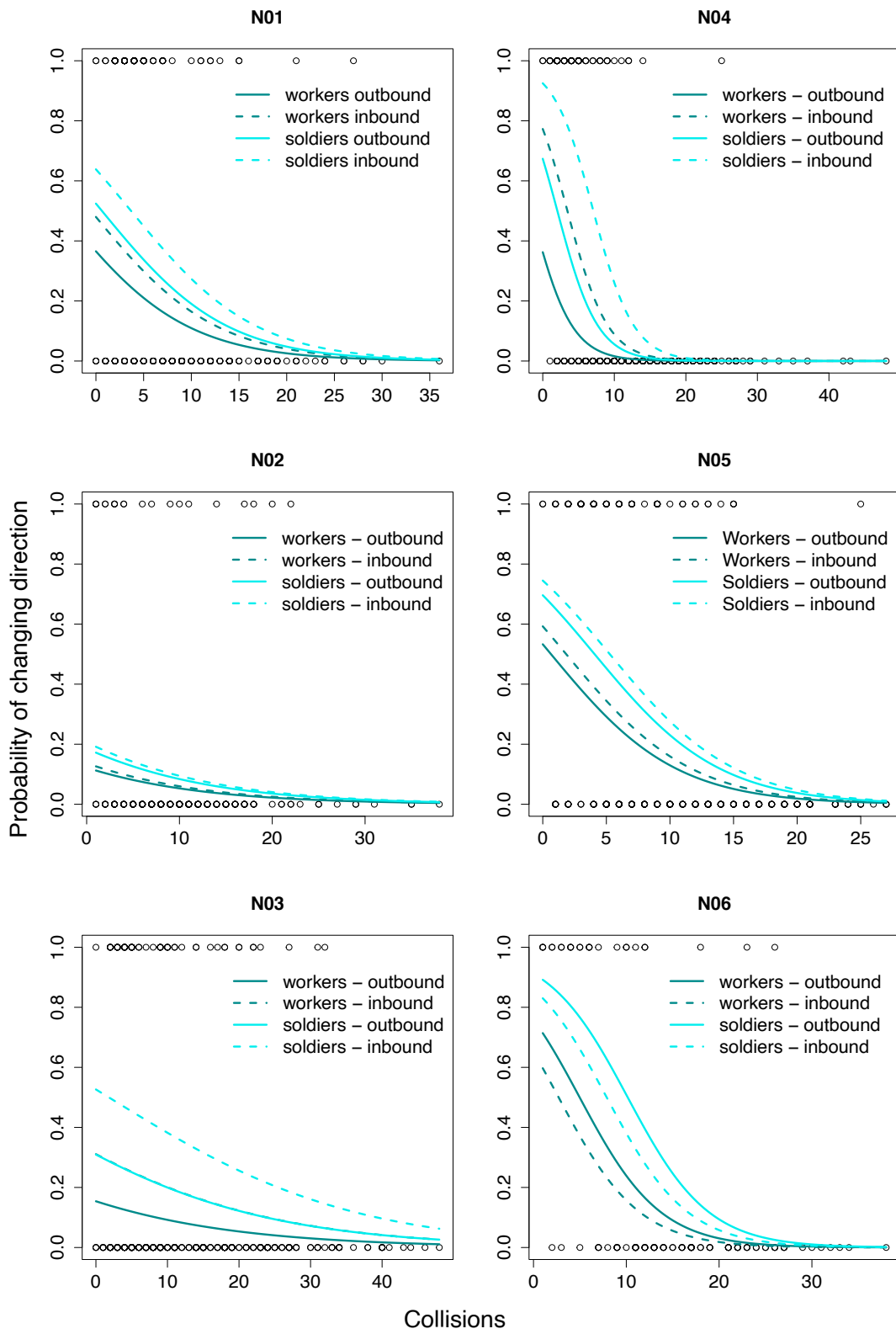
	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight
N08	4	0.22	-0.16	+		3	-67.7	141.6	1.49	0.24
	7	0.07	-0.17		+	3	-68.0	142.2	2.02	0.18
	3	0.50	-0.199			2	-127.2	258.4	0.00	0.32
	7	0.57	-0.186		+	3	-126.4	258.9	0.52	0.24
N09	4	0.61	-0.191	+		3	-126.4	258.9	0.57	0.22
	8	0.71	-0.177	+	+	4	-125.5	259.2	0.85	0.21
	6	-0.39		+	+	3	-139.5	285.0	26.6	0.00
N10	8	0.24	-0.142	+	+	4	-96.1	200.5	0.00	0.35
	4	0.35	-0.123	+		3	-97.4	201.0	0.48	0.28
	7	0.50	-0.134		+	3	-97.8	201.7	1.21	0.19
	3	0.58	-0.117			2	-98.9	201.9	1.40	0.18
	1	-0.79				1	-109.3	220.6	20.13	0.00
N11	4	0.51	-0.160	+		3	-66.8	139.8	0.00	0.65
	8	0.47	-0.162	+	+	4	-66.8	141.8	2.05	0.24
	7	0.17	-0.14		+	3	-88.4	183.0	0.0	0.70
N12	8	0.27	-0.14	+	+	4	-88.2	184.7	1.7	0.30
	5	-0.68			+	2	-96.8	197.6	14.6	0.00
N13	7	0.10	-0.149		+	3	-126.6	259.3	0.00	0.53
	8	0.17	-0.146	+	+	4	-126.4	260.9	1.60	0.24
	3	0.32	-0.137			2	-128.8	261.7	2.38	0.16
N14	5	-0.30			+	2	-52.0	108.1	0.00	0.38
	7	-0.02	-0.033		+	3	-51.4	109.0	0.93	0.24
	6	-0.05		+	+	3	-51.4	109.0	0.93	0.24
	8	0.17	-0.029	+	+	4	-51.0	110.3	2.23	0.12
N15	3	0.54	-0.208			2	-96.3	196.7	0.00	0.42
	4	0.64	-0.199	+		3	-95.7	197.6	0.90	0.27
	7	0.60	-0.202		+	3	-96.1	198.3	1.59	0.19
	8	0.70	-0.193	+	+	4	-95.5	199.2	2.48	0.12
N16	4	0.49	-0.217	+		3	-65.3	136.7	0.00	0.36
	3	0.10	-0.204			2	-66.5	137.1	0.34	0.31
	8	0.36	-0.222	+	+	4	-65.0	138.2	1.49	0.17
	7	-0.03	-0.211		+	3	-66.1	138.4	1.65	0.16
	1	-1.48				1	-75.1	152.3	15.52	0.00
N17	4	0.59	-0.191	+		3	-120.2	246.6	0.00	0.57
	8	0.68	-0.183	+	+	4	-119.7	247.6	1.01	0.34
	3	0.34	-0.202			2	-123.5	250.9	4.37	0.06
	8	0.82	-0.142	+	+	4	-44.7	97.7	0.00	0.53
	7	0.43	-0.142		+	3	-46.0	98.2	0.48	0.42

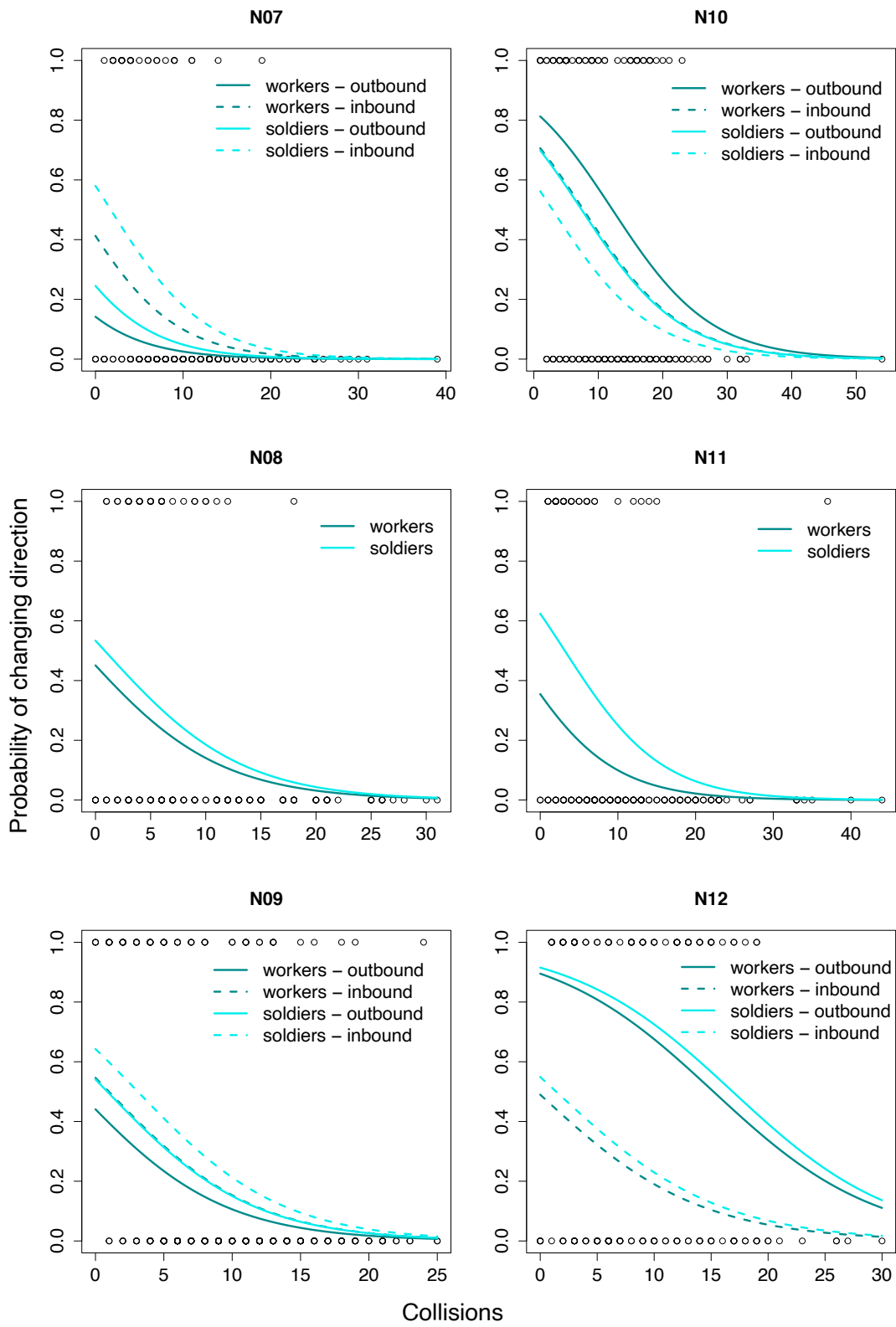
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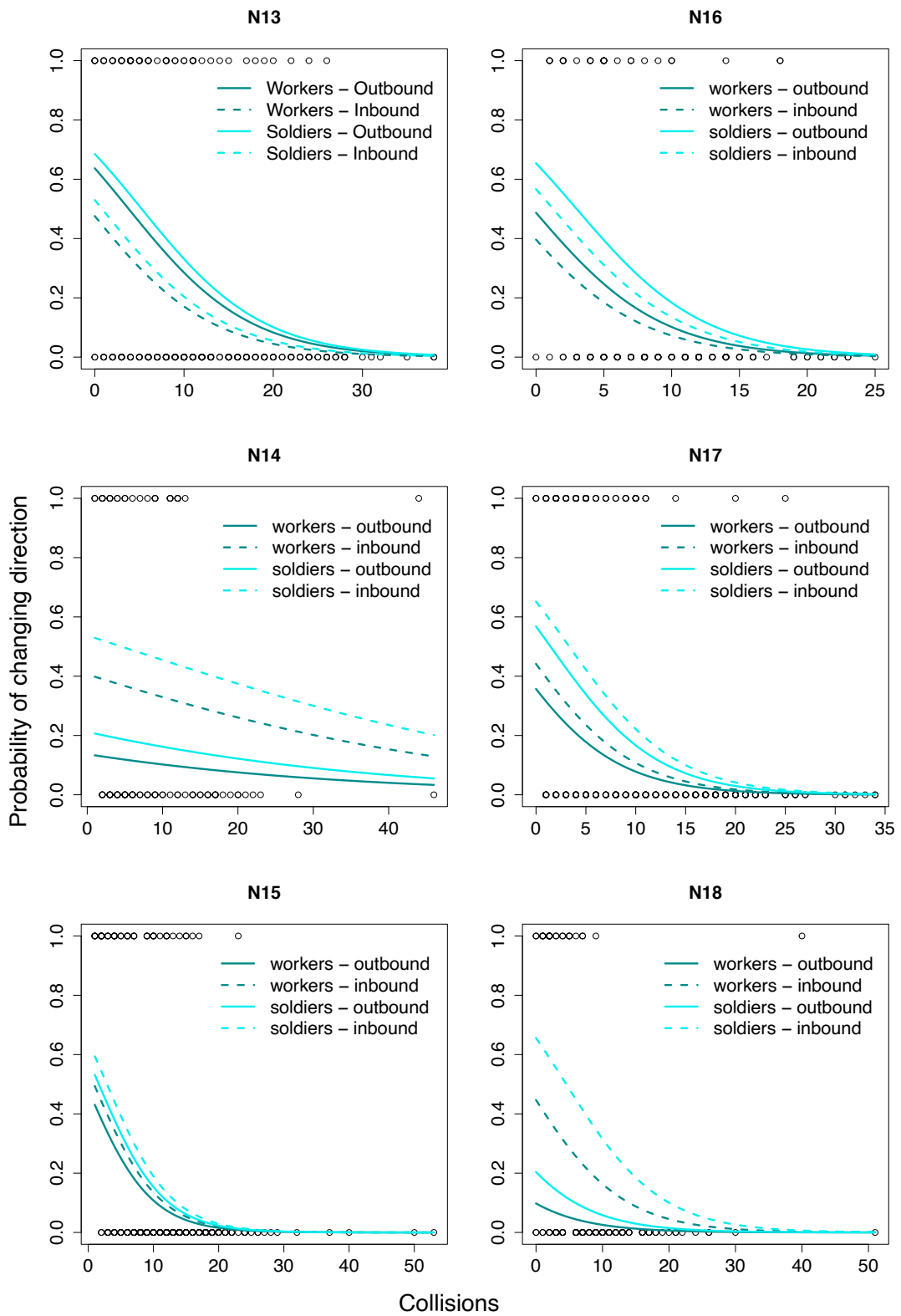
∞ \underline{Z}_i	id (Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight
\underline{Z}_6	-0.01		+	+	3	-49.1	104.4	6.65	0.02

4.1.2 Plots

Figures of the effect of collisions on the termites' propensity to reverse the traffic direction. Collisions mean the frontal encounter between individuals moving in opposite directions. Increments in contacts faced by individuals triggered a decrease in the probability of change the movement orientation.







4.2 Appendix II: propensity of termites halt

4.2.1 Statistical models

Table 4.2: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of collisions on the termites' propensity to halt while walking in a foraging trail. Column headings: id = model identification, (Intrc) = model intercept, cllsn = number of head-on encounters (collisions) between termites moving in opposite directions, caste = caste of the focal termite (worker or soldier), drctn = direction of movement of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight	
N01	5	-3.33			+	2	-50.8	105.7	0.00	0.33	
	1	-2.71				1	-52.4	106.9	1.20	0.18	
	7	-3.16	-0.030			+	3	-50.6	107.3	1.66	0.14
	6	-3.21		+	+	3	-50.7	107.5	1.84	0.13	
	2	-2.59		+		2	-52.3	108.7	3.02	0.07	
N02	2	-3.03		+		2	-25.9	55.8	0.00	0.27	
	1	-3.54				1	-27.3	56.6	0.80	0.18	
	6	-3.44		+	+	3	-25.5	57.2	1.36	0.14	
	4	-2.64	-0.044	+		3	-25.7	57.5	1.72	0.11	
	3	-2.94	-0.063			2	-26.9	58.0	2.13	0.09	
N03	8	-0.51	-0.042	+	+	4	-110.4	228.9	0.00	0.61	
	4	-0.23	-0.035	+		3	-112.6	231.3	2.36	0.19	
N04	2	-2.77		+		2	-44.1	92.2	0.00	0.37	
	4	-2.12	-0.067	+		3	-43.2	92.5	0.33	0.31	
	6	-2.87		+	+	3	-44.0	94.1	1.93	0.14	
	8	-2.24	-0.068	+	+	4	-43.1	94.4	2.22	0.12	
N05	4	-1.47	-0.108	+		3	-49.4	104.9	0.00	0.43	
	8	-1.69	-0.123	+	+	4	-48.8	105.8	0.89	0.28	
	2	-2.37		+		2	-51.4	106.9	2.01	0.16	
	6	-2.55		+	+	3	-51.2	108.6	3.67	0.07	
N06	2	-2.96		+		2	-12.0	28.0	0.00	0.27	
	4	-1.74	-0.106	+		3	-11.2	28.7	0.63	0.20	
	1	-3.56				1	-13.7	29.5	1.47	0.13	
	6	-2.60		+	+	3	-11.7	29.7	1.65	0.12	
	3	-2.23	-0.114			2	-12.8	29.8	1.72	0.11	
	8	-1.38	-0.110	+	+	4	-11.0	30.4	2.38	0.08	
N07	2	-2.77		+		2	-28.4	60.9	0.00	0.38	
	6	-2.95		+	+	3	-28.3	62.8	1.87	0.15	
	4	-2.99	0.021	+		3	-28.4	62.8	1.93	0.15	

Table 4.2 continued from previous page

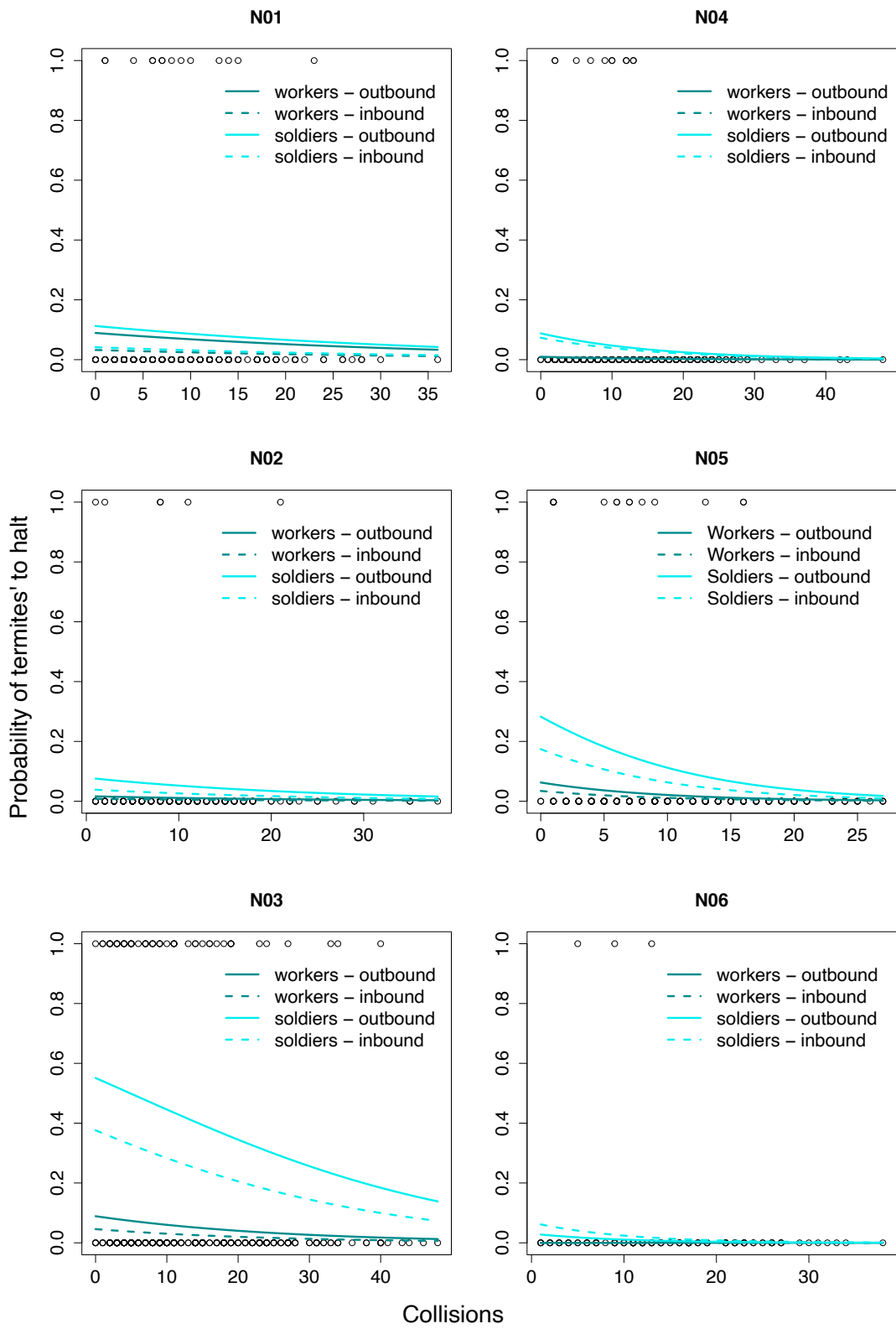
	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight
	1	-3.33				1	-30.4	62.8	1.95	0.14
	5	-3.50			+	2	-30.3	64.7	3.82	0.06
	6	-21.73		+	+	3	-7.7	21.5	0.00	0.27
	5	-21.57			+	2	-9.1	22.2	0.69	0.19
N08	2	-3.61		+		2	-9.2	22.6	1.08	0.16
	1	-4.29				1	-10.6	23.2	1.72	0.11
	8	-21.73	-0.001	+	+	4	-7.7	23.6	2.11	0.09
	3	-2.46	-0.177			2	-26.7	57.5	0.00	0.24
	4	-2.24	-0.148	+		3	-25.8	57.7	0.26	0.21
N09	2	-3.24		+		2	-27.2	58.4	0.92	0.15
	1	-3.76				1	-28.6	59.3	1.80	0.10
	7	-2.44	-0.172		+	3	-26.7	59.5	2.03	0.09
	8	-2.21	-0.140	+	+	4	-25.8	59.8	2.26	0.08
	7	-20.00	-0.412		+	3	-3.9	14.0	0.00	0.19
	1	-5.16				1	-6.2	14.4	0.32	0.17
	3	-3.05	-0.261			2	-5.4	14.8	0.76	0.13
N10	5	-22.57			+	2	-5.5	15.0	0.98	0.12
	2	-4.47		+		2	-5.5	15.0	0.98	0.12
	8	-20.37	-0.353	+	+	4	-3.6	15.4	1.40	0.10
	4	-2.37	-0.272	+		3	-4.7	15.6	1.58	0.09
	6	-22.69		+	+	3	-4.8	15.7	1.65	0.09
	2	-1.84		+		2	-37.4	78.9	0.00	0.53
N11	6	-1.95		+	+	3	-37.3	80.8	1.92	0.20
	4	-1.84	0.00	+		3	-37.4	80.9	2.08	0.19
	1	-5.00				1	-6.0	14.0	0.00	0.22
	3	-3.31	-0.326			2	-5.3	14.7	0.64	0.16
	2	-4.34		+		2	-5.4	14.8	0.74	0.15
N12	5	-4.41			+	2	-5.4	14.9	0.87	0.14
	4	-2.62	-0.337	+		3	-4.6	15.5	1.41	0.11
	6	-3.76		+	+	3	-4.8	15.7	1.67	0.10
	7	-3.29	-0.255		+	3	-5.1	16.3	2.24	0.07
	2	-3.06		+		2	-24.5	53.0	0.00	0.49
N13	4	-2.77	-0.031	+		3	-24.4	54.8	1.80	0.20
	6	-3.06		+	+	3	-24.5	55.1	2.05	0.18
	8	-2.80	-0.032	+	+	4	-24.4	56.9	3.84	0.07
N14	1	-26.57				1	-0.0	2.0	0.00	0.41
	2	-26.57		+		2	-0.0	4.1	2.09	0.14
	1	-3.88				1	-24.4	50.9	0.00	0.32
	3	-3.09	-0.072			2	-24.0	52.0	1.10	0.19
N15	2	-3.69		+		2	-24.3	52.7	1.83	0.13
	5	-4.10			+	2	-24.3	52.7	1.83	0.13
	7	-3.30	-0.085		+	3	-23.7	53.6	2.68	0.08
	2	-2.76		+		2	-24.2	52.6	0.00	0.27

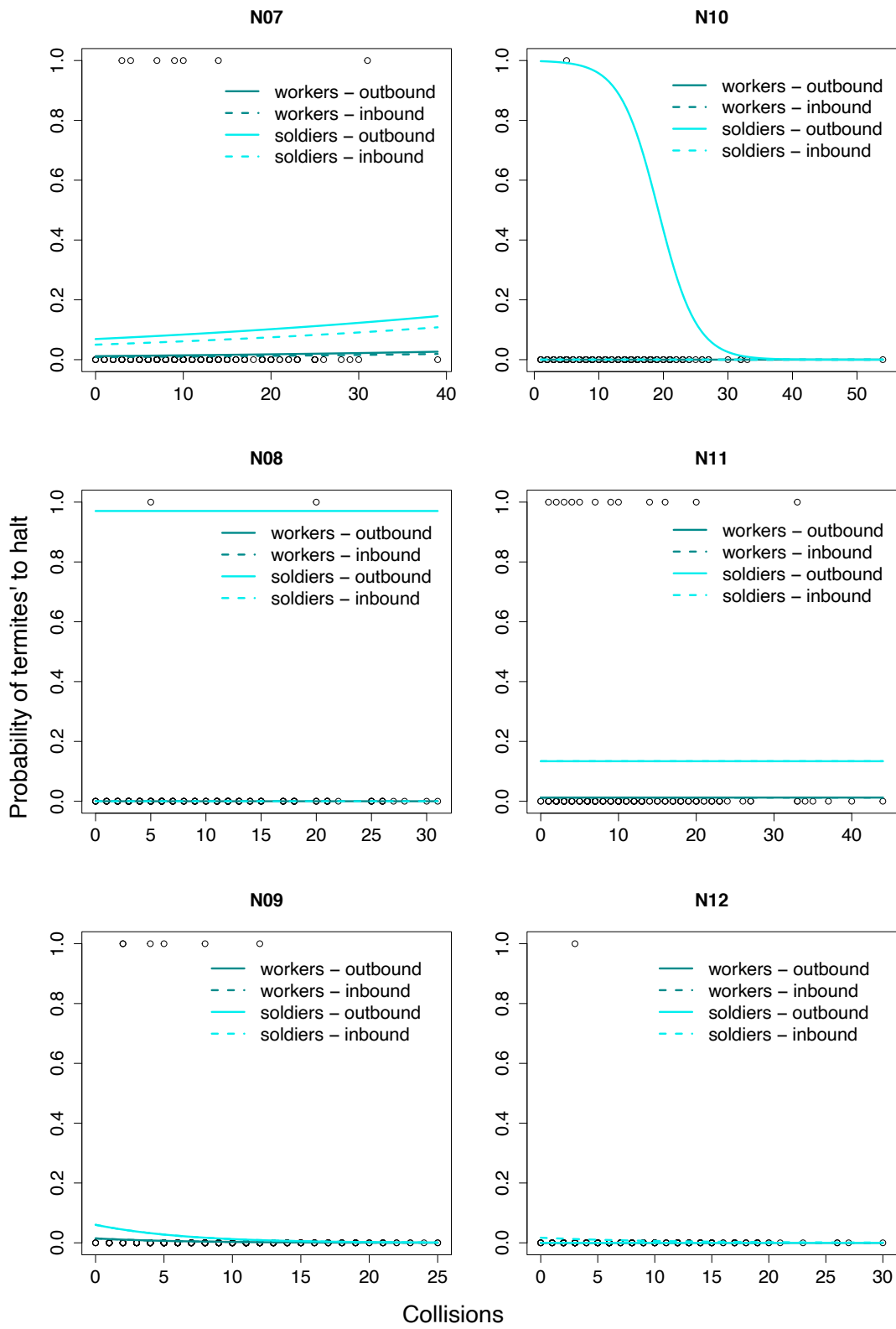
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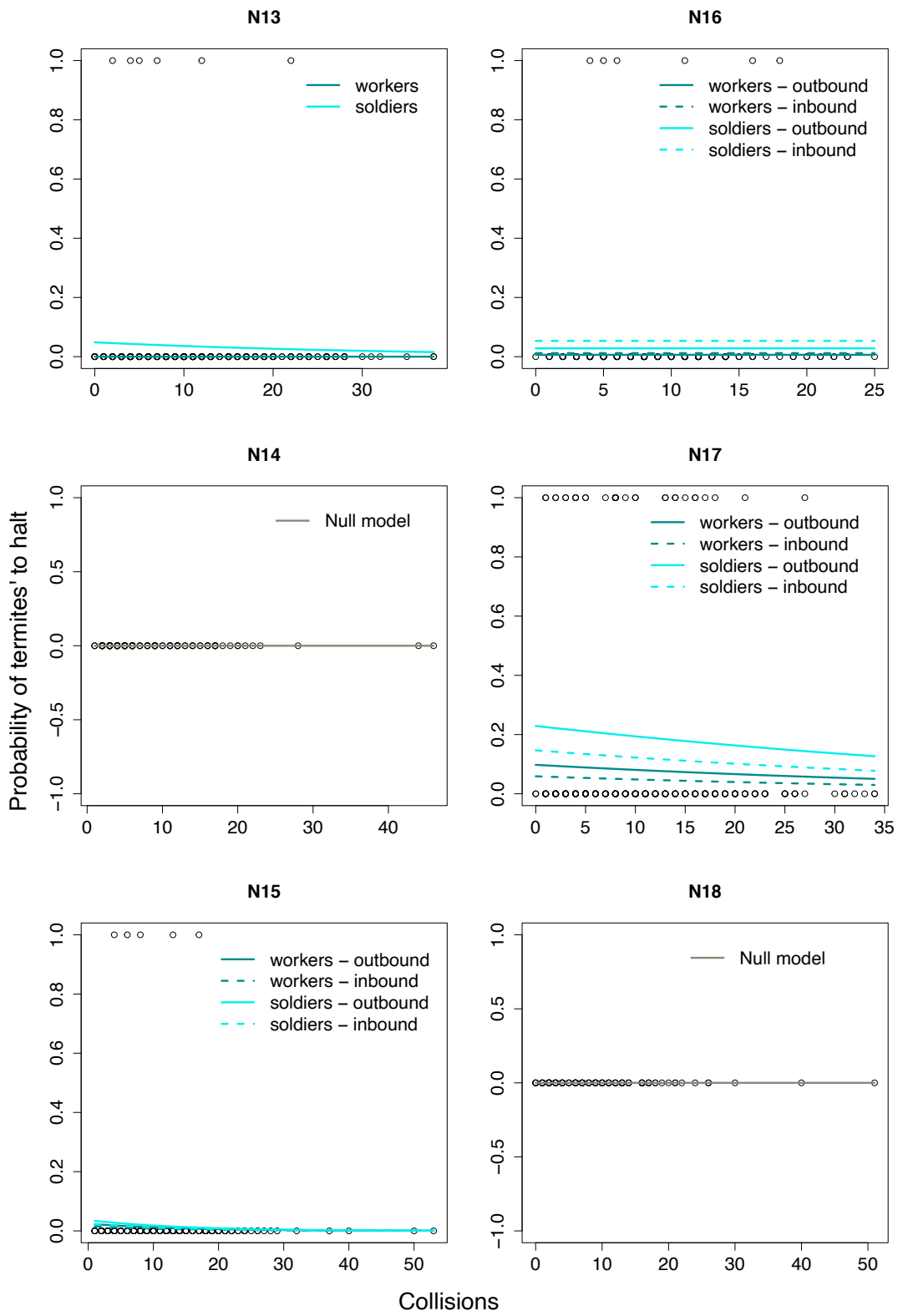
	id	(Intrc)	cllsn	caste	drctn	df	logLik	AICc	Δ	weight
	1	-3.23				1	-25.5	53.0	0.41	0.22
N16	6	-2.46		+	+	3	-23.9	54.0	1.43	0.13
	5	-2.97			+	2	-25.2	54.5	1.93	0.10
	4	-2.92	0.016	+		3	-24.2	54.6	2.04	0.10
	2	-1.68		+		2	-97.3	198.6	0.00	0.32
	6	-1.95		+	+	3	-96.4	198.8	0.27	0.28
N17	8	-1.76	-0.027	+	+	4	-96.0	200.1	1.50	0.15
	4	-1.55	-0.014	+		3	-97.1	200.4	1.80	0.13
	7	-1.99	-0.046		+	3	-98.5	203.2	4.61	0.03
N18	1	-26.57				1	-0.0	2.0	0.00	0.40
	2	-26.57		+		2	-0.0	4.1	2.07	0.14

4.2.2 Plots

The probability of termites' halt decrease with the increments in the number of collisions. In most cases, termite soldiers had more tendency to stop than workers.







4.3 Appendix III: Speed

4.3.1 Statistical models

Table 4.3: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the effect of collisions on termites' mean speed along the foraging platform. Column headings: id = model identification, (Intrc) = model intercept, cllsn = number of face-face encounters (collisions) between termites moving in opposite directions, cllsn² = quadratic form of collisions, caste = caste of the focal termite (worker or soldier), drctn = movement orientation of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

	id	(Intrc)	cllsn	cllsn ²	caste	drctn	df	logLik	AICc	Δ	weight
N01	1	-0.14					2	-76.9	157.9	0.00	0.21
	7	-0.25	0.022	-7.8e-04			4	-75.3	158.8	0.87	0.14
	3	-0.17	0.003				3	-76.7	159.5	1.55	0.10
	5	-0.15		2.0e-05			3	-76.9	160.0	2.04	0.08
	9	-0.14				+	3	-76.9	160.0	2.04	0.08
	2	-0.14			+		3	-76.9	160.0	2.05	0.08
	15	-0.25	0.027	-8.7e-04			+	5	-74.9	160.2	2.22
N02	16	-0.23	0.039	-1.4e-03	+	+	6	9.6	-6.7	0.00	0.46
	15	-0.22	0.041	-1.4e-03		+	5	8.4	-6.4	0.30	0.39
	8	-0.25	0.037	-1.3e-03	+		5	6.8	-3.3	3.43	0.08
N03	4	-0.10	-0.006		+		4	-138.5	285.2	0.00	0.34
	8	-0.06	-0.014	2.1e-04	+		5	-137.9	286.1	0.92	0.21
	12	-0.10	-0.006		+	+	5	-138.5	287.1	1.98	0.13
	6	-0.15		-1.3e-04	+		4	-139.5	287.2	2.04	0.12
N04	16	-0.24	0.023	-8.0e-04	+	+	6	51.8	-91.3	0.00	1.00
	15	-0.21	0.023	-8.0e-04		+	5	45.1	-80.1	11.21	0.00
N05	16	-0.29	0.043	-0.001	+	+	6	-60.1	132.6	0.00	0.89
	8	-0.32	0.040	-0.001	+		5	-64.1	138.3	5.73	0.05
N06	15	-0.55	0.069	-0.00		+	5	0.2	10.2	0.00	0.56
	16	-0.56	0.069	-0.00	+	+	6	0.3	12.4	2.22	0.19
N07	4	-0.00	-0.013		+		4	-22.8	53.8	0.00	0.36
	12	-0.01	-0.014		+	+	5	-22.5	55.2	1.40	0.18
	6	-0.07		-4.4e-04	+		4	-23.8	55.8	1.98	0.13
	8	0.00	-0.015	6.4e-05	+		5	-22.8	55.9	2.07	0.13
	9	-0.10				+	3	-48.1	102.4	0.00	0.17
	11	-0.04	-0.007			+	4	-47.2	102.7	0.37	0.14

Table 4.3 continued from previous page

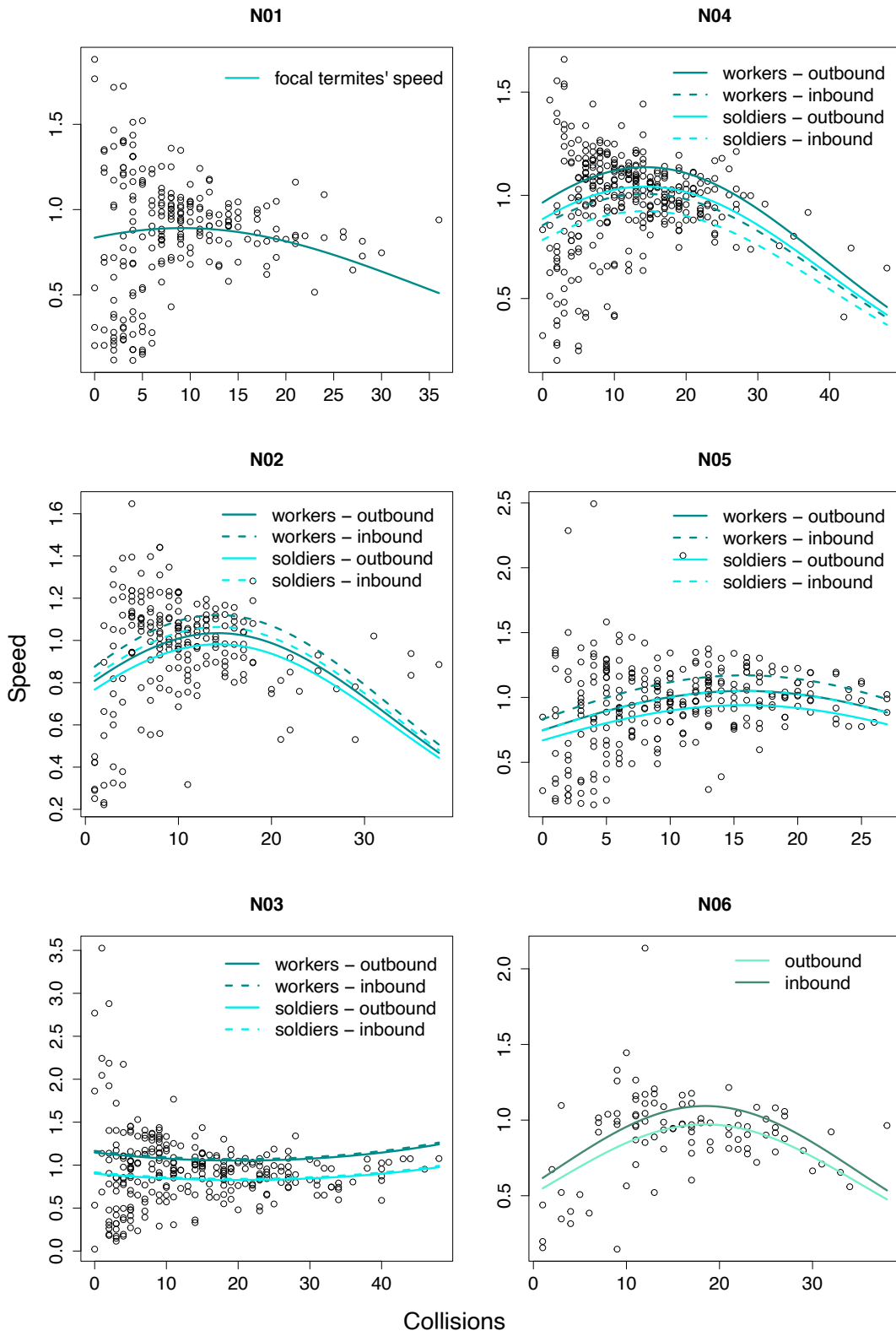
	id	(Intrc)	cllsn	cllsn ²	caste	drctn	df	logLik	AICc	Δ	weight
N08	12	-0.08	-0.007		+	+	5	-46.2	102.8	0.39	0.14
	10	-0.14			+	+	4	-47.3	102.8	0.47	0.13
	16	-0.01	-0.029	0.008	+	+	6	-45.2	103.0	0.62	0.13
	15	0.03	-0.025	0.007		+	5	-46.5	103.4	0.99	0.10
	13	-0.08		-0.002		+	4	-47.7	103.7	1.32	0.09
	14	-0.12		-0.002	+	+	5	-46.8	104.0	1.60	0.08
	8	-0.02	-0.041	0.001	+		5	-49.6	109.6	7.22	0.00
N09	16	-0.43	0.063	-2.5e-03	+	+	6	44.7	-77.2	0.00	0.36
	8	-0.43	0.060	-2.5e-03	+		5	43.3	-76.4	0.73	0.25
	15	-0.41	0.065	-2.6e-03		+	5	43.3	-76.4	0.76	0.25
	7	-0.42	0.062	-2.5e-03			4	41.7	-75.2	2.00	0.13
	4	-0.22	0.006		+		4	26.0	-43.9	33.30	0.00
N10	8	-0.53	0.051	-1.5e-03	+		5	41.8	-73.2	0.00	0.38
	7	-0.50	0.051	-1.5e-03			4	40.5	-72.7	0.44	0.30
	16	-0.52	0.052	-1.5e-03	+	+	6	42.1	-71.6	1.56	0.17
	15	-0.50	0.052	-1.5e-03		+	5	40.8	-71.3	1.88	0.15
	3	-0.24	0.007				3	26.5	-46.9	26.28	0.00
N11	10	-0.16			+	+	4	-18.6	45.5	0.00	0.32
	16	-0.25	0.017	-4.2e-04	+	+	6	-16.6	45.7	0.17	0.29
	12	-0.18	0.003		+	+	5	-18.1	46.6	1.11	0.18
	14	-0.16		0.00	+	+	5	-18.6	47.5	1.99	0.12
	15	-0.21	0.022	2.9e-05		+	5	-19.7	49.9	4.34	0.04
N12	15	-0.32	0.047	-0.002		+	5	17.4	-24.4	0.00	0.61
	16	-0.30	0.047	-0.002	+	+	6	18.0	-23.5	0.93	0.38
	11	-0.19	0.011			+	4	11.3	-14.2	10.18	0.00
N13	15	-0.07	0.026	-8.7e-04		+	5	-106.2	222.6	0.00	0.37
	16	-0.09	0.026	-8.7e-04	+	+	6	-105.6	223.5	0.93	0.24
	9	0.06				+	3	-109.8	225.6	3.07	0.08
N14	9	-0.22				+	3	-10.6	27.4	0.00	0.24
	1	-0.15					2	-12.2	28.5	1.12	0.14
	10	-0.19			+	+	4	-10.3	29.0	1.66	0.10
	11	-0.22	0.001			+	4	-10.5	29.5	2.13	0.08
N15	16	-0.42	0.043	-1.2e-03	+	+	6	51.4	-90.5	0.00	0.42
	8	-0.43	0.041	-1.2e-03	+		5	49.9	-89.5	1.07	0.25
	15	-0.41	0.045	-1.3e-03		+	5	49.8	-89.3	1.27	0.22
	7	-0.42	0.044	-1.2e-03			4	48.0	-87.9	2.64	0.11
N16	8	-0.40	0.041	-1.8e-03	+		5	9.5	-8.7	0.00	0.42
	16	-0.38	0.041	-1.8e-03	+	+	6	10.5	-8.5	0.16	0.39
	10	-0.20			+	+	4	6.4	-4.6	4.09	0.05
	16	-0.20	0.027	-9.2e-04	+	+	6	-36.6	85.5	0.00	0.87

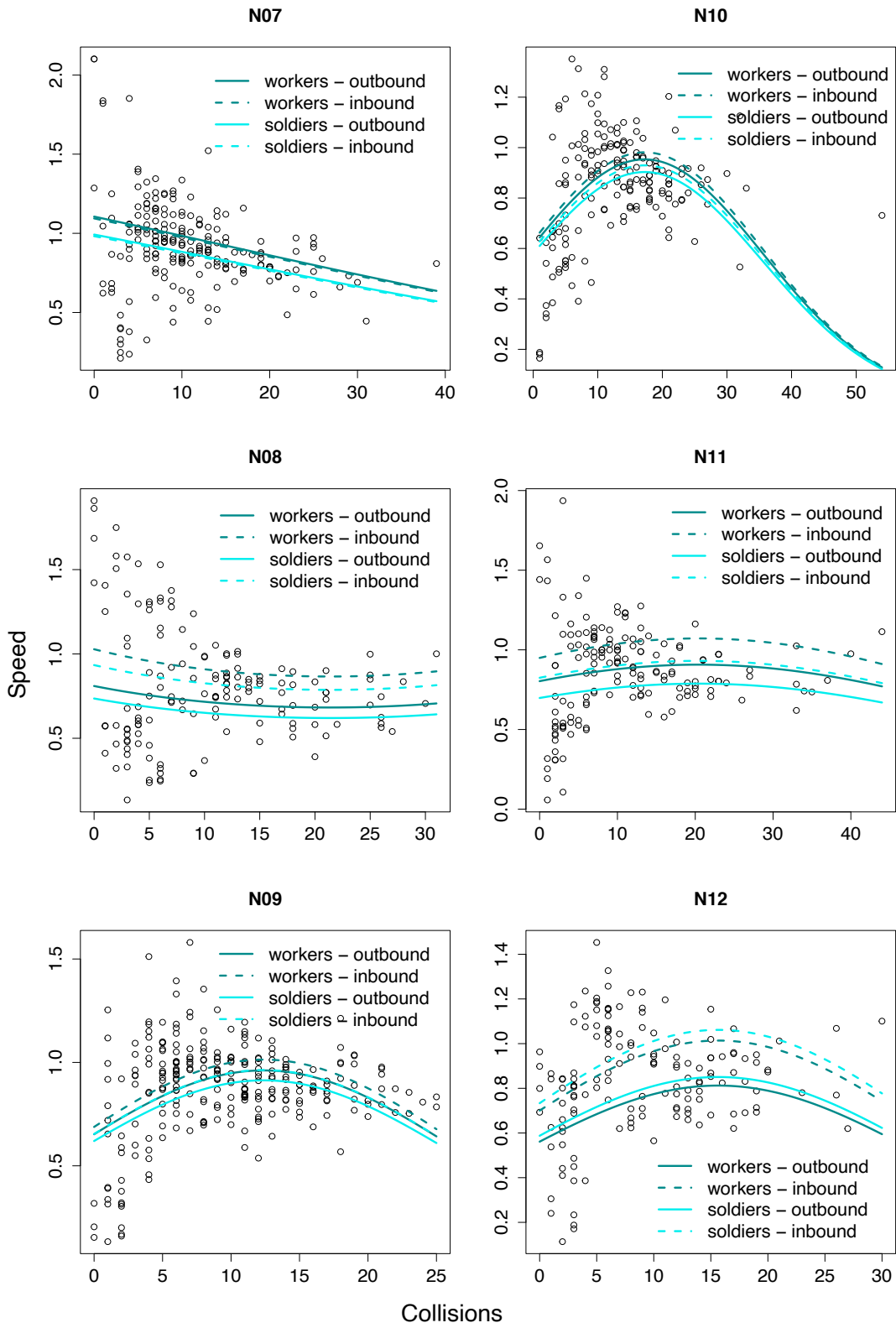
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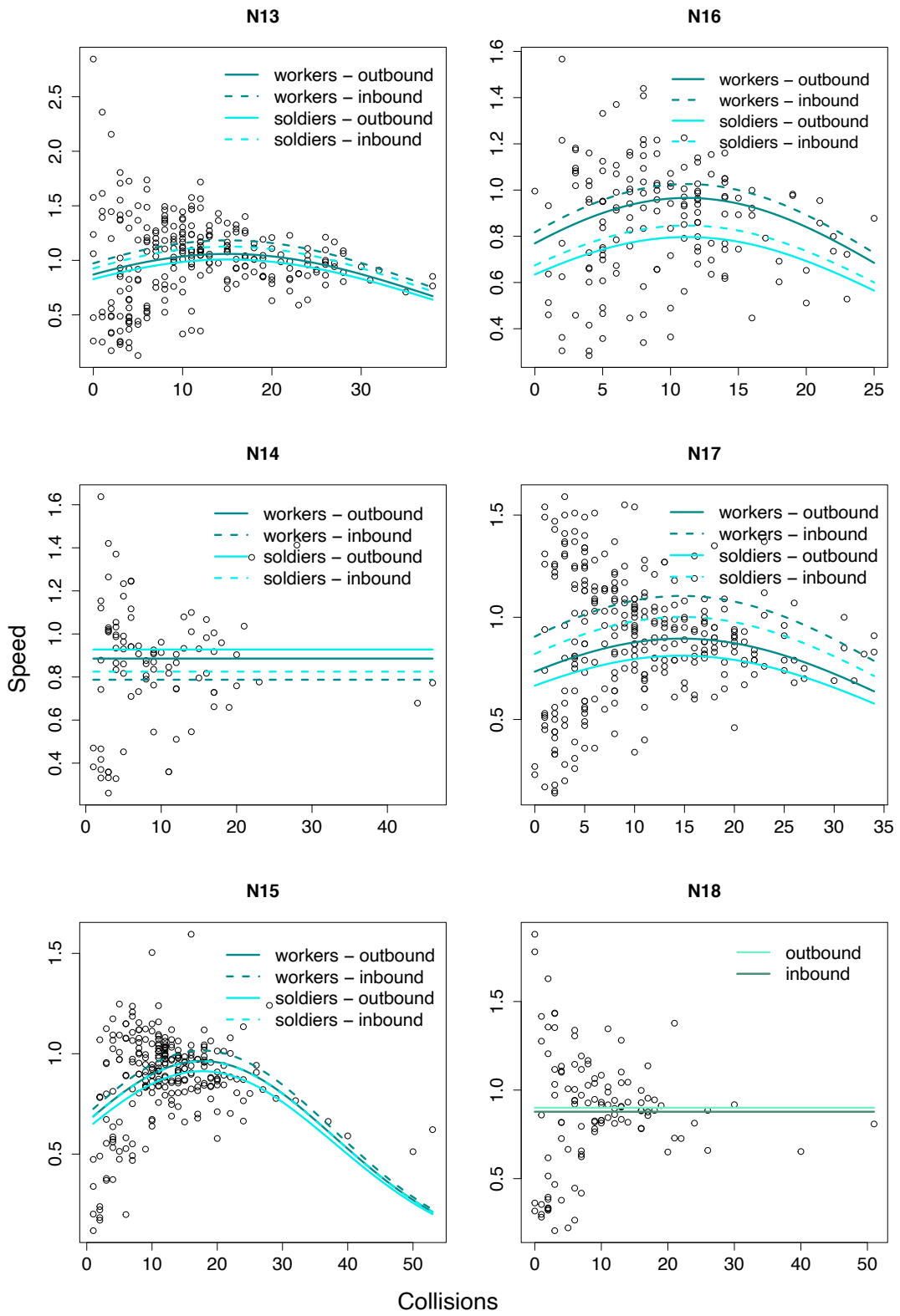
	id	(Intrc)	cllsn	cllsn ²	caste	drctn	df	logLik	AICc	Δ	weight
N17	15	-0.17	0.030	-9.5e-04		+	5	-40.1	90.3	4.85	0.08
	1	-0.13					2	-34.1	72.2	0.00	0.28
N18	9	-0.14				+	3	-34.0	74.2	1.98	0.10
	5	-0.12		-3.3e-05			3	-34.0	74.3	2.02	0.10

4.3.2 Plots

Termites modulated their speed in a function of the number of collisions with nestmates. Under lower collisions, termites were stimulated to increase their speed. Under higher collisions, the mean speed of individuals decreased. Termite workers frequently moved faster than soldiers. The inbound lane favored higher speeds.







4.4 Appendix IV: speed and collisions during the foraging episode

4.4.1 Statistical models

Table 4.4: Models with substantial empirical evidence ($\Delta \leq 2$) predicting the dynamic of collisions and speed during the foraging episode. The time was measured as the hours elapsed from the starting of the foraging. Column headings: id = model identification, (Intrc) = model intercept, time = time in hours elapsed from the beginning of foraging episode, time² = quadratic form of the time elapsed, caste = caste of the focal termite (worker or soldier), drctn = movement orientation of the focal termite (inbound or outbound), df = degree of freedom, logLik = log-likelihood, AICc = second-order Akaike information criterion, Δ = AICc difference between the model in concern and the best model. weight = Akaike weight.

	id	(Intrc)	time	time ²	caste	drctn	df	logLik	AICc	Δ	weight
N01	13	-0.06	-0.116	0.015			4	-60.9	129.9	0.00	0.53
	14	-0.07	-0.116	0.015	+		5	-60.8	131.9	1.96	0.20
	15	-0.06	-0.116	0.015		+	5	-60.9	132.0	2.08	0.19
N02	2	-0.07			+		3	-3.7	13.5	0.00	0.18
	4	-0.05			+	+	4	-2.7	13.5	0.03	0.18
	1	-0.04					2	-5.4	14.8	1.35	0.09
	3	-0.01				+	3	-4.4	15.0	1.49	0.09
	6	-0.07	-0.001		+		4	-3.7	15.6	2.07	0.06
	10	-0.07		2.9e-05	+		4	-3.7	15.6	2.07	0.06
N03	14	-0.20	-0.091	0.018	+		5	-114.4	239.1	0.00	0.49
	16	-0.18	-0.089	0.018	+	+	6	-114.2	240.7	1.64	0.22
	10	-0.36		0.009	+		4	-116.4	240.9	1.79	0.20
	12	-0.34		0.009	+	+	5	-116.1	242.4	3.30	0.09
N04	16	-0.07	-0.056	0.007	+	+	6	43.2	-74.1	0.00	0.89
	12	-0.16		0.054	+	+	5	39.6	-68.9	5.13	0.07
N05	12	-0.11		0.002	+	+	5	-68.9	148.1	0.00	0.22
	16	-0.02	-0.049	0.007	+	+	6	-68.1	148.5	0.39	0.18
	8	-0.12	0.013		+	+	5	-69.5	149.2	1.15	0.12
	10	-0.14		0.002	+		4	-70.6	149.2	1.18	0.12
	14	-0.05	-0.050	0.007	+		5	-69.7	149.5	1.45	0.10
	4	-0.07			+	+	4	-70.7	149.6	1.54	0.10
	6	-0.16	0.013		+		4	-71.1	150.4	2.33	0.07
N06	15	2.92	-0.802	0.052		+	5	-6.9	24.4	0.00	0.59
	16	2.89	-0.798	0.052	+	+	6	-6.9	26.7	2.23	0.19
	16	-0.17	-0.072	0.012	+	+	6	19.7	-26.9	0.00	0.54

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	id	(Intrc)	time	time ²	caste	drctn	df	logLik	AICc	Δ	weight
N07	14	-0.19	-0.074	0.012	+		5	18.4	-26.5	0.41	0.44
	13	-0.13	-0.074	0.012			4	12.9	-17.6	9.28	0.01
N08	16	0.03	-0.287	0.035	+	+	6	-1.2	15.1	0.00	0.61
	15	0.07	-0.285	0.035		+	5	-2.8	16.0	0.93	0.38
	14	-0.03	-0.308	0.038	+		5	-7.7	25.8	10.67	0.00
N09	14	-0.11	-0.038	0.004	+		5	25.7	-41.1	0.00	0.24
	2	-0.17			+		3	23.5	-40.9	0.19	0.22
	10	-0.19		0.001	+		4	24.0	-39.8	1.26	0.13
	6	-0.19	0.003		+		4	23.6	-39.1	2.00	0.09
	16	-0.12	-0.038	0.004	+	+	6	25.7	-39.0	2.09	0.09
N10	14	-0.08	-0.081	0.010	+		5	27.0	-43.6	0.00	0.19
	16	-0.11	-0.081	0.010	+	+	6	27.9	-43.4	0.27	0.17
	13	-0.05	-0.082	0.010			4	25.7	-43.1	0.54	0.14
	15	-0.07	-0.081	0.010		+	5	26.6	-42.8	0.83	0.12
	2	-0.20			+		3	23.8	-41.6	2.07	0.07
N11	16	-0.01	-0.16	0.02	+	+	6	-7.1	26.7	0.0	0.60
	14	-0.04	-0.17	0.02	+		5	-8.6	27.6	1.0	0.37
	15	0.07	-0.16	0.02		+	5	-11.9	34.1	7.5	0.01
N12	15	0.01	-0.097	0.013		+	5	8.2	-6.0	0.00	0.18
	3	-0.11				+	3	5.9	-5.7	0.31	0.16
	16	0.04	-0.095	0.012	+	+	6	8.9	-5.3	0.73	0.13
	7	-0.06	-0.016			+	4	6.8	-5.2	0.77	0.12
	4	-0.09			+	+	4	6.6	-4.9	1.08	0.11
	8	-0.03	-0.017		+	+	5	7.6	-4.8	1.24	0.10
	11	-0.09		-0.015		+	4	6.3	-4.3	1.69	0.08
12	-0.06		-0.018	+	+	5	7.1	-3.8	2.25	0.06	
N13	8	-0.27	0.053		+	+	5	-65.6	141.4	0.00	0.55
	16	-0.31	0.073	-0.002	+	+	6	-65.2	142.7	1.32	0.28
	7	-0.22	0.051			+	4	-68.3	144.8	3.40	0.10
N14	15	0.07	-0.349	0.072		+	5	-4.3	19.3	0.00	0.42
	13	0.13	-0.355	0.073			4	-5.9	20.3	1.02	0.25
	16	0.09	-0.348	0.073	+	+	6	-4.0	20.9	1.66	0.18
	14	0.15	-0.354	0.072	+		5	-5.6	21.9	2.63	0.11
	10	-0.22		0.001	+		4	32.3	-56.4	0.00	0.34
	6	-0.25	0.012		+		4	31.7	-55.2	1.22	0.18
	12	-0.21		0.001	+	+	5	32.5	-54.7	1.65	0.15

Table 4.4 continued from previous page

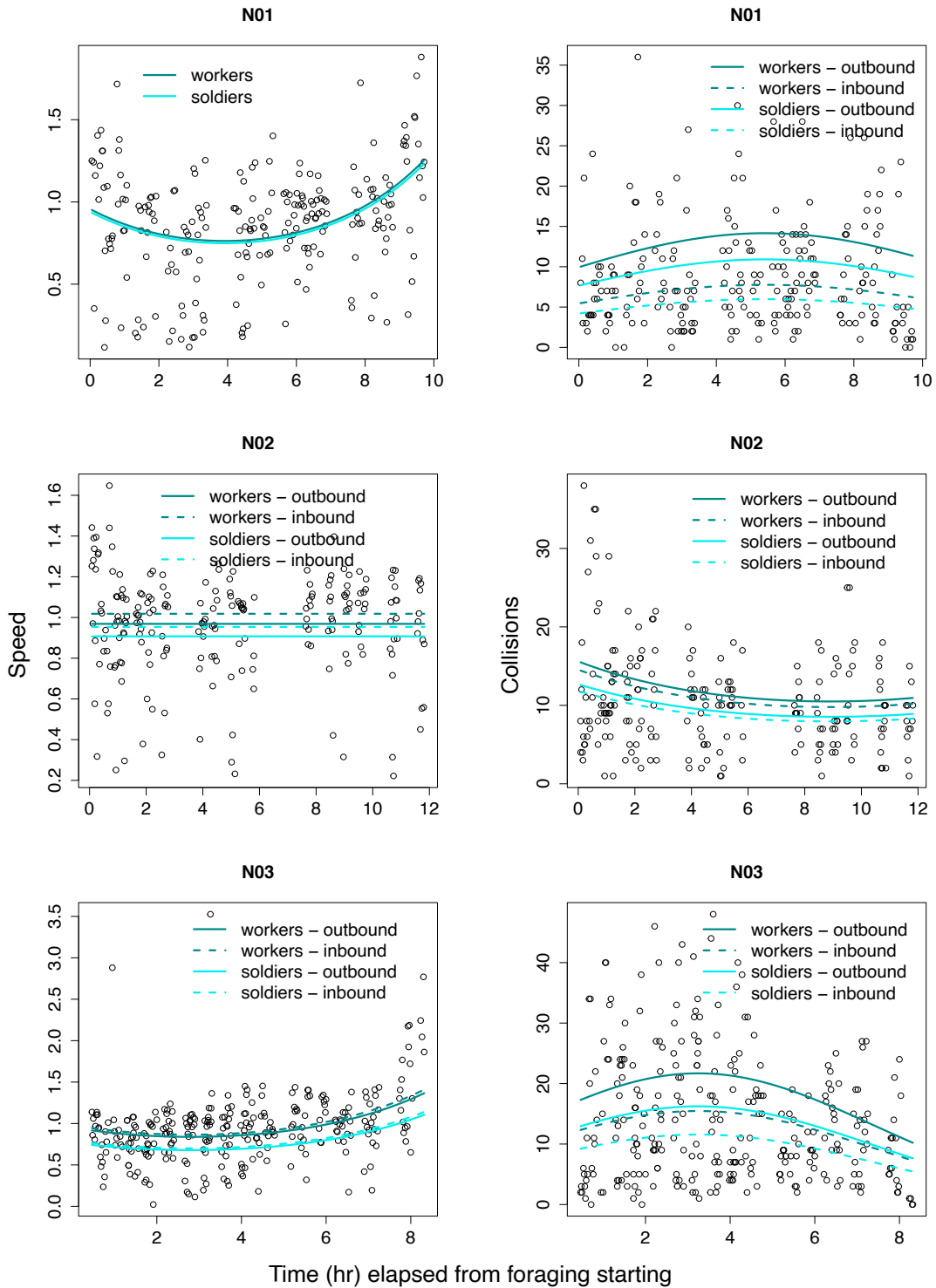
	id	(Intrc)	time	time ²	caste	drctn	df	logLik	AICc	Δ	weight		
Collisions	N15	14	-0.21	-0.006	0.001	+		5	32.3	-54.4	1.95	0.13	
		8	-0.24	0.012		+	+	5	31.9	-53.5	2.91	0.08	
	N16	16	-0.01	-0.115	0.013	+	+	6	11.5	-10.4	0.00	0.46	
		14	-0.05	-0.117	0.014	+		5	10.2	-10.0	0.42	0.37	
		8	-0.12	-0.020		+	+	5	8.3	-6.2	4.21	0.06	
	N17	8	-0.32	0.036		+	+	5	-14.7	39.7	0.00	0.68	
		16	-0.33	0.040	-3.2e10 ⁻⁴	+	+	6	-14.7	41.7	2.03	0.25	
	N18	13	0.08	-0.271	0.044			4	-19.9	48.1	0.00	0.55	
		14	0.06	-0.271	0.044	+		5	-19.8	50.2	2.04	0.20	
	Collisions	N01	16	1.44	0.130	-0.012	+	+	5	-818.3	1646.9	0.00	1.00
			8	1.61	0.015		+	+	4	-825.5	1659.2	12.38	0.00
		N02	16	2.45	-0.088	0.005	+	+	5	-789.9	1590.0	0.00	0.52
			14	2.49	-0.089	0.005	+		4	-791.3	1590.7	0.68	0.37
			8	2.37	-0.033		+	+	4	-793.0	1594.2	4.13	0.07
		N03	16	2.14	0.190	-0.029	+	+	5	-1513.8	3037.9	0.00	1.00
			12	2.45		-0.007	+	+	4	-1532.0	3072.2	34.32	0.00
		N04	16	2.21	0.135	-0.019	+	+	5	-1445.3	2900.8	0.00	0.66
			14	2.24	0.1333	-0.018	+		4	-1447.0	2902.2	1.36	0.34
12			2.43		-0.003	+	+	4	-1457.7	2923.5	22.68	0.00	
N05		16	1.41	0.328	-0.030	+	+	5	-1045.1	2100.4	0.00	1.00	
		15	1.50	0.326	-0.030		+	4	-1055.5	2119.2	18.82	0.00	
N06		8	3.34	-0.093		+	+	4	-411.5	831.4	0.00	0.22	
		6	3.39	-0.093		+		3	-412.9	832.0	0.60	0.16	
		12	2.99		-0.006	+	+	4	-411.8	832.0	0.61	0.16	
		10	3.05		-0.006	+		3	-413.2	832.6	1.18	0.12	
		16	3.72	-0.199	0.007	+	+	5	-411.4	833.4	1.98	0.08	
		14	3.75	-0.192	0.007	+		4	-412.8	834.0	2.56	0.06	
N07	16	1.95	0.141	-0.019	+	+	5	-700.6	1411.5	0.00	0.97		
	15	2.01	0.142	-0.019		+	4	-705.0	1418.3	6.78	0.03		
N08	16	1.78	0.274	-0.032	+	+	5	-613.1	1236.5	0.00	0.79		
	15	1.83	0.277	-0.032		+	4	-615.4	1239.1	2.60	0.21		
N09	16	1.93	0.050	-0.007	+	+	5	-901.0	1812.3	0.00	0.64		
	12	2.03		-0.003	+	+	4	-902.7	1813.6	1.34	0.33		
	8	2.05	-0.023		+	+	4	-905.0	1818.1	5.79	0.04		

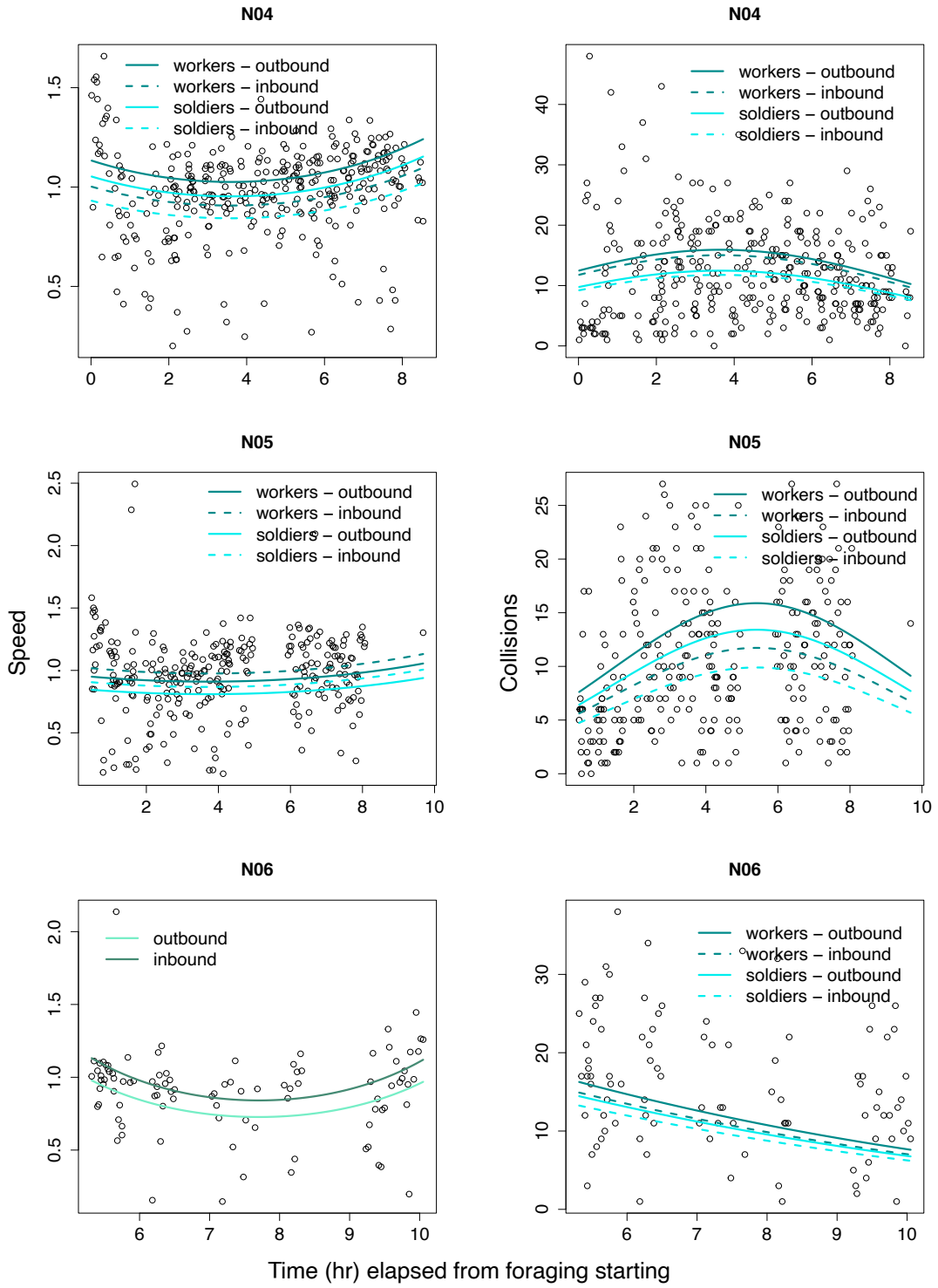
Table 4.4 continued from previous page

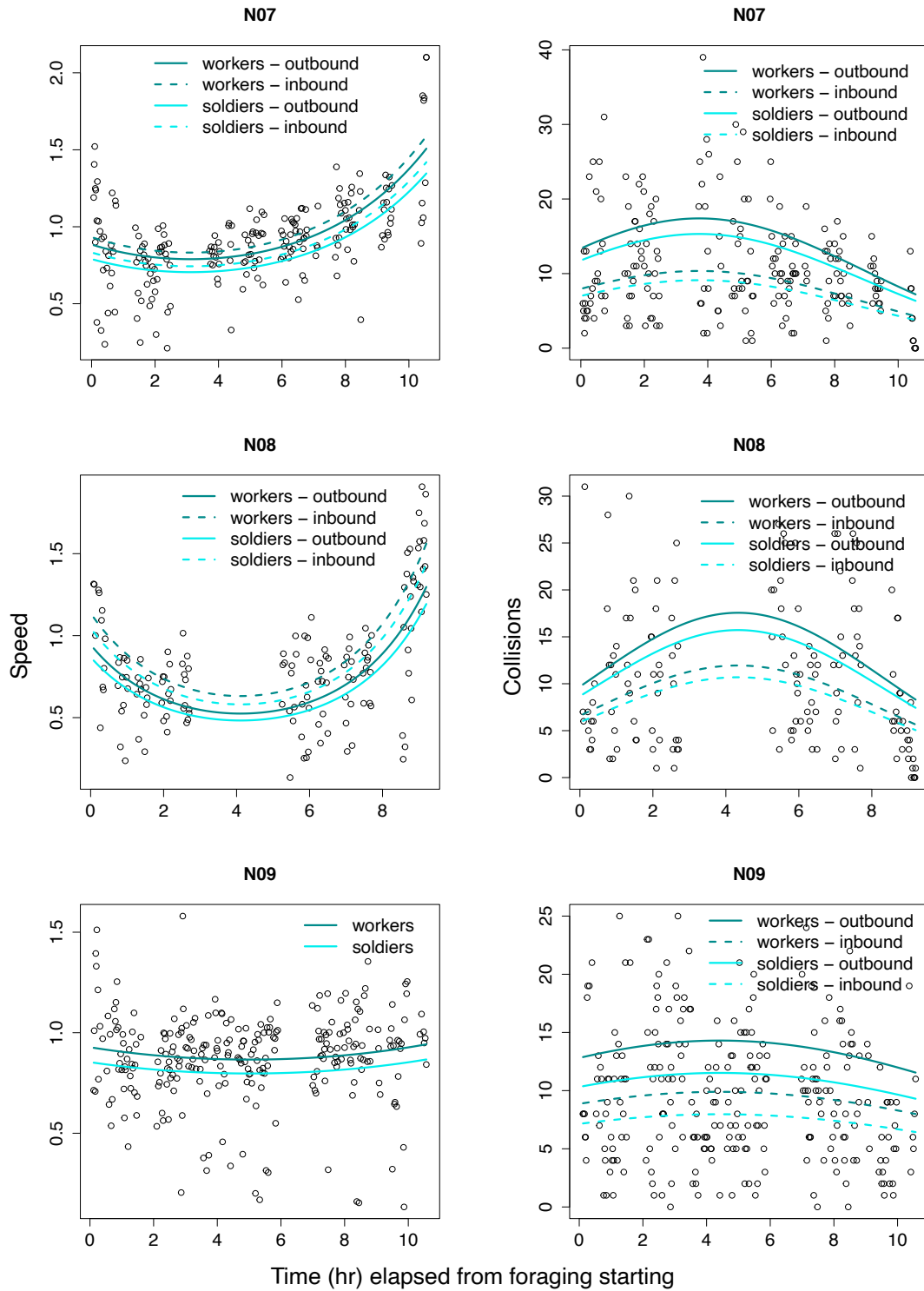
	id	(Intrc)	time	time ²	caste	drctn	df	logLik	AICc	Δ	weight
N10	16	2.48	-0.079	0.007	+	+	5	-727.0	1464.3	0.00	0.49
	8	2.40	-0.022		+	+	4	-728.4	1465.1	0.74	0.34
	12	2.36		-0.002	+	+	4	-729.5	1467.3	2.96	0.11
N11	16	2.16	0.150	-0.025	+	+	5	-746.2	1502.8	0.00	1.00
	12	2.37		-0.008	+	+	4	-753.4	1515.1	12.37	0.00
N12	15	2.04	0.192	-0.054		+	4	-519.1	1046.5	0.00	0.73
	16	2.04	0.192	-0.054	+	+	5	-519.1	1048.6	2.14	0.25
N13	16	2.06	0.132	-0.015	+	+	5	-1087.8	2185.8	0.00	1.00
	12	2.31		-0.004	+	+	4	-1109.4	2227.1	41.26	0.00
N14	14	2.66	-0.507	0.083	+		4	-406.9	822.3	0.00	0.59
	16	2.61	-0.502	0.083	+	+	5	-406.2	823.0	0.71	0.41
	6	2.39	-0.125		+		3	-415.0	836.2	13.93	0.00
N15	16	2.58	-0.075	0.003	+	+	5	-948.5	1907.3	0.00	0.82
	8	2.51	-0.038		+	+	4	-951.1	1910.3	3.00	0.18
N16	16	2.10	0.164	-0.031	+	+	5	-509.1	1028.6	0.00	0.75
	15	2.05	0.161	-0.031		+	4	-511.3	1030.9	2.33	0.23
N17	16	1.80	0.145	-0.014	+	+	5	-1130.0	2270.3	0.00	1.00
	12	2.14		-0.003	+	+	4	-1157.4	2322.9	52.63	0.00
N18	16	2.32	-0.206	0.019	+	+	5	-510.1	1030.7	0.00	0.77
	8	2.19	-0.081		+	+	4	-512.4	1033.3	2.53	0.22

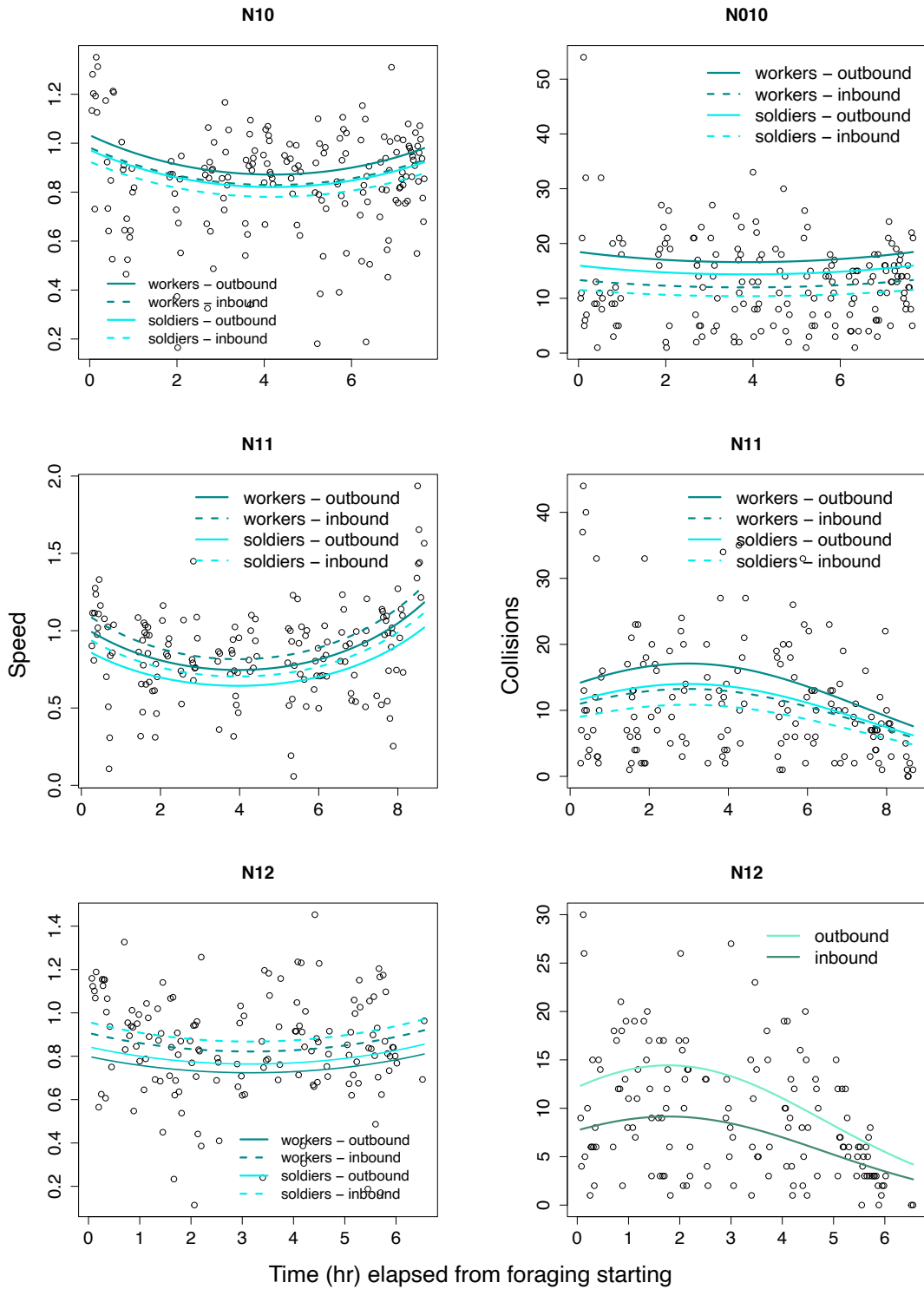
4.4.2 Plots

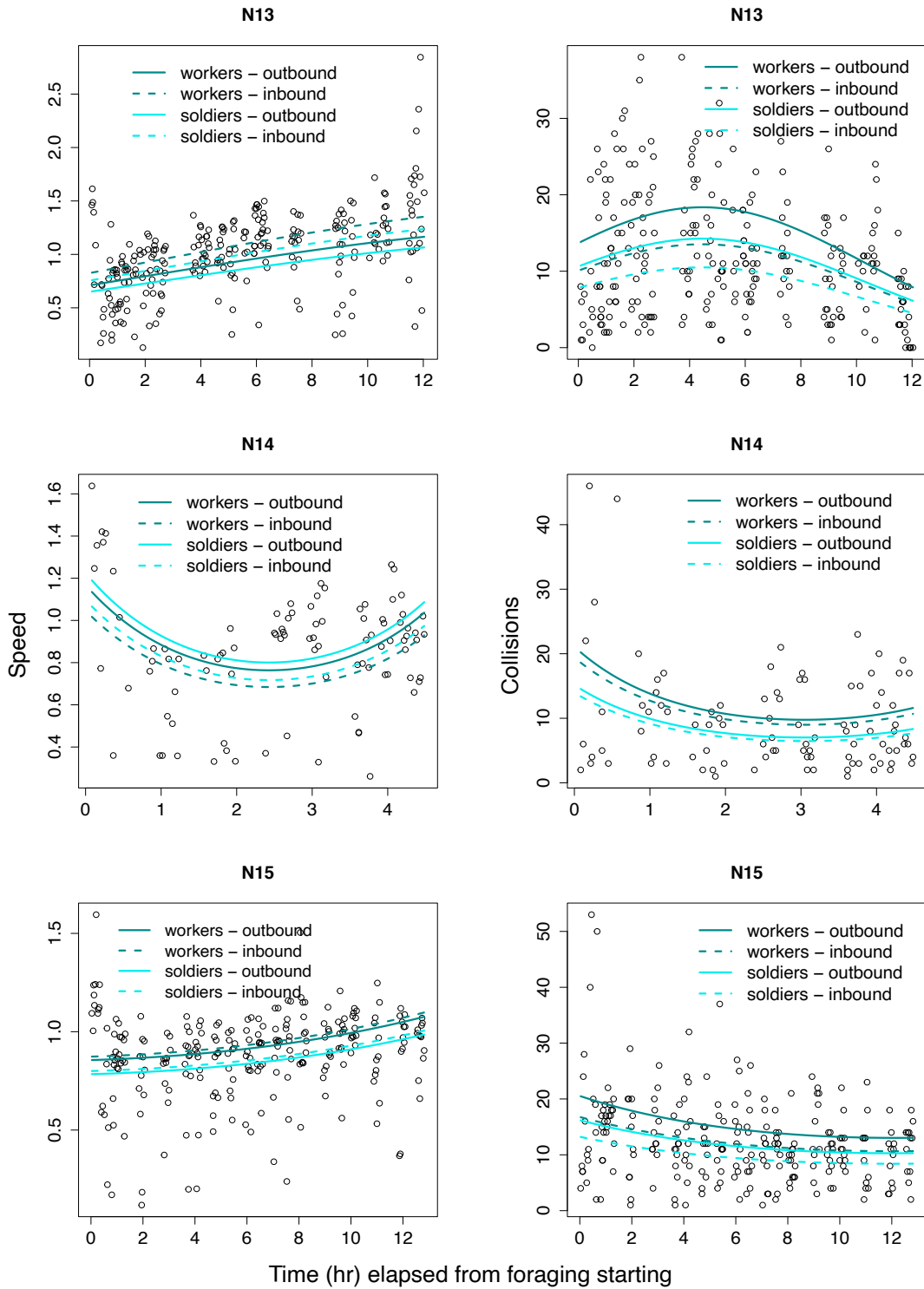
The dynamic of speed and collisions during the foraging behaved like a mirror with inverse and complementary patterns. There is a quadratic and negative correlation between speed and the time elapsed from the beginning of foraging.



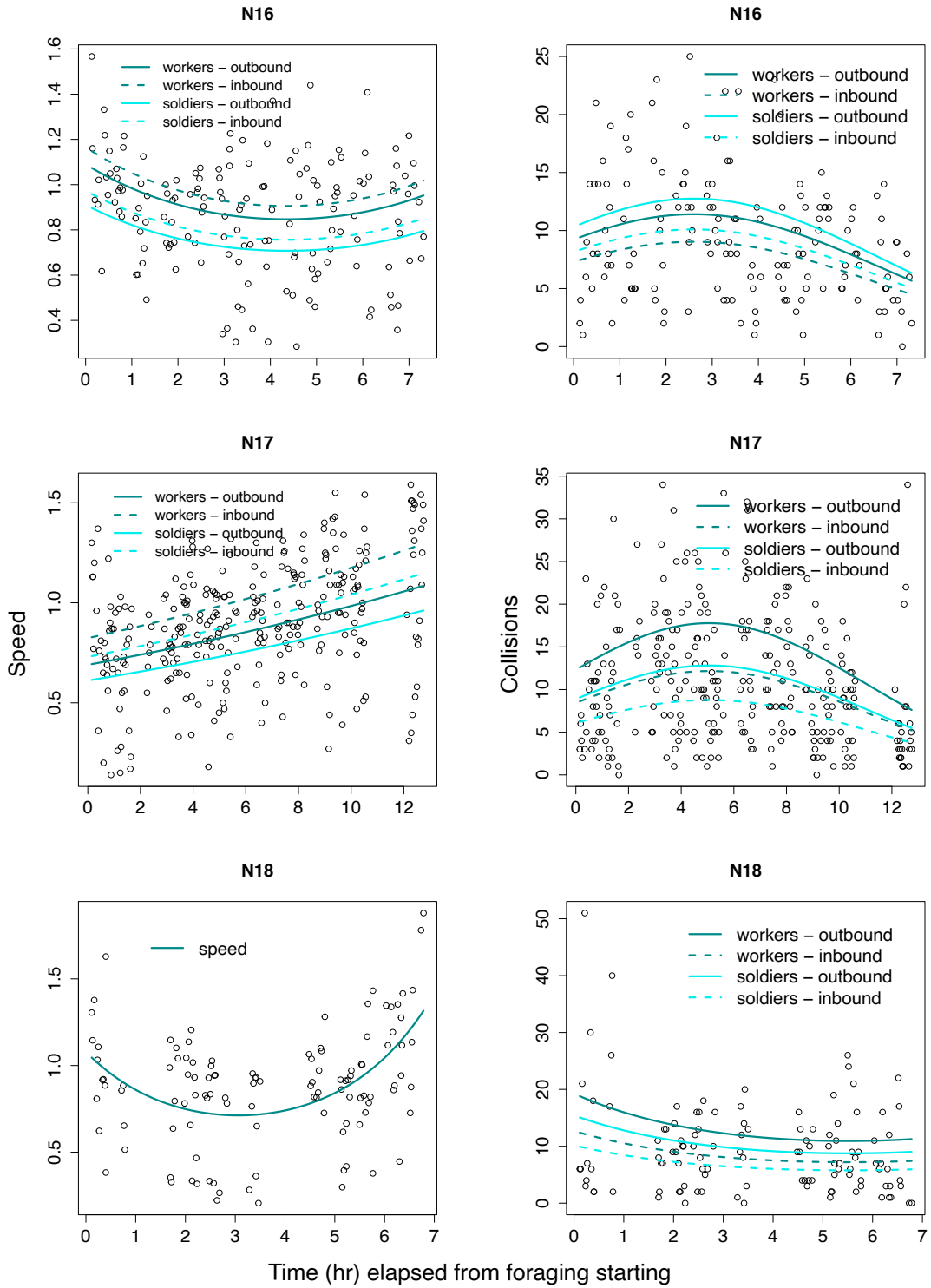








Time (hr) elapsed from foraging starting



Time (hr) elapsed from foraging starting