EFECTO DE LA HETEROGENEIDAD ESPACIAL DE PAISAJE Y USO DE INFORMACIÓN SOBRE LAS CONDUCTAS DE LOCOMOCIÓN Y FORRAJEO EN INSECTOS SOCIALES

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Dedicado a

mis abuelos Ana y Hugo

por el amor incondicional que me entregaron

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RESUMEN

La locomoción y alimentación son comportamientos importantes para la adecuación biológica de los organismos. En general, estas actividades son desarrolladas en hábitats espacialmente heterogéneos, y son dependientes además de la capacidad de percepción de los individuos. En la literatura está bien documentado que las restricciones físicas del paisaje (e.g. factores abióticos, cobertura vegetacional) determinan trayectorias con ciertos patrones espaciales (e.g. desplazamientos lineales y/o complejos). Sin embargo, este conocimiento ha sido escasamente conectado con: i) el estímulo (e.g. alimento, pareja reproductiva, depredadores) que desencadena los desplazamientos, ii) la adquisición de información acerca del ambiente externo que realizan los organismos durante el forrajeo y la locomoción, y iii) el efecto que tendría el desempeño locomotor sobre otras conductas como el éxito de forrajeo. El objetivo de esta tesis fue evaluar la existencia de una relación causal entre el desempeño locomotor y el éxito de forrajeo en insectos sociales como las hormigas, la cual sería modulada por la heterogeneidad espacial de paisaje y el procesamiento de información de estos organismos. Tanto el forrajeo como el movimiento de los individuos han sido generalmente tratados en la literatura como conductas independientes entre sí. El modelo de forrajeo en lugar central, constituyó una aproximación teórica que permitió evaluar los compromisos y restricciones que operan sobre las conductas exhibidas por los animales en la matriz entre parches de recursos. En términos generales, los resultados encontrados en trabajos de campo y laboratorio con *Dorymyrmex goetschi*, *Pogonomyrmex barbatus*, *Camponotus morosus* y *C. chilensis* muestran que una mayor heterogeneidad espacial de paisaje

incrementó las distancias recorridas y los tiempos de viaje, y disminuyó las velocidades de locomoción de las obreras. Un mayor número de contactos antenales produjo un aumento en las tasas de remoción de recursos a nivel de la colonia, y a medida que los individuos adquirían información del entorno, el desempeño locomotor incrementó. Las vías de movimiento con menores distancias recorridas, tiempos de viaje cortos, y altas velocidades de locomoción tuvieron un efecto positivo sobre el éxito de forrajeo. Estos resultados fueron comunes para especies de hormigas que diferían en la escala espacial de sus desplazamientos (e.g. 0.5 m *vs.* 16.0 m), hábitos tróficos (e.g. generalistas *vs.* especialistas), y estrategias utilizadas para explotar los recursos (e.g. grupal *vs.* individual). Atributos de las hormigas como el grano grueso de percepción y el uso de reglas simples, determinarían la toma de decisiones acerca de la ejecución de tareas de forrajeo por parte de la colonia. En particular, los antecedentes sugieren que la utilización de señales visuales (e.g. marcas familiares, luz polarizada) y/o mecanismos químicos de comunicación (e.g. hidrocarburos de cutícula, feromonas de camino) entre obreras, jugarían un papel importante en las conductas de reclutamiento y orientación hacia fuentes de alimento y en la posterior explotación de los recursos.

ABSTRACT

Locomotion and foraging are important behaviors with potential fitness consequences to the animals. These behaviors are performed in heterogeneous habitats, and are dependent on the information achieved by individuals in the environment. It is well documented that habitat structure restricts the trajectories of animals due to physical barriers that impede movement. Nevertheless, this knowledge has not been linked to: i) the stimulus that triggers movements, ii) the changes that trajectories experience through time as a result of information accumulation, and iii) the influence of locomotion on the foraging behavior performance. The aim of this thesis was to evaluate a causal relationship between locomotion performance and foraging success in social insects like ants, which would be modulated by landscape spatial heterogeneity and information processing of organisms. Traditionally, locomotion and foraging behaviors have been studied as independent events. The central place foraging model allowed the experimental study of effects that both a matrix of spatial heterogeneity and information use have on food transportation and movement trajectories of organisms. In general terms, my fieldwork and laboratory results with *Dorymyrmex goetschi*, *Pogonomyrmex barbatus*, *Camponotus morosus* y *C. chilensis* revealed that greater landscape spatial heterogeneity increased path length and travel time, and diminished locomotion velocity of worker ants. A greater number of antennal contacts increased resource removal rate by the colony and, as individuals acquired information from their environment, locomotion performance increased. Movements with shorter path lengths and travel times, and greater locomotion velocities increased foraging success. These results were

common for species of ants that differed in the spatial scale of their displacements, feeding habits and strategies used to exploit resources. Attributes of ants as the coarse grain of perception and the use of rules of the thumb, determine the decision to carry out foraging tasks at the colony level. Specifically, previous information suggest that the use of visual signals (e.g. familiar marks, polarized light) and chemical mechanisms of communication (e.g. cuticle hydrocarbons, trail pheromones) between workers, would play an important role in recruitment and guidance towards food sources, and later, in the exploitation of resources.

INTRODUCCIÓN GENERAL

Conductas de locomoción y alimentación.-

Entre las conductas más importantes para la adecuación biológica de los organismos se encuentran la locomoción y la alimentación. El desplazamiento locomotor permite, por ejemplo, la búsqueda de refugios y/o parejas reproductivas, y la alimentación permite satisfacer las demandas energéticas y nutritivas de los individuos (Bell 1990, Krebs & Davies 1993, Wehner 1997). Estas actividades son desarrollas en hábitats espacialmente heterogéneos en términos de distribución y abundancia de recursos tróficos, condiciones microclimáticas, competidores, depredadores, estructura de la vegetación y elementos físicos abióticos (Southwood 1977, Kolasa & Rollo 1991, Kozakiewicz 1995). Además, el nivel de resolución sensorial de los individuos (i.e. la distancia de detección de diferentes elementos del ambiente durante el desplazamiento) determina el tipo de heterogeneidad espacial al cual se confrontan (Milne 1991, Allen & Hoekstra 1991, With 1994b, Zollner & Lima 1997). De esta forma, el paisaje constituye el escenario donde interactúan componentes de la heterogeneidad espacial del hábitat con la capacidad de percepción de los organismos, lo cual afecta sus conductas de movimiento y forrajeo (Kozakiewicz 1995, Lima & Zollner 1996).

El desplazamiento de los organismos es un fenómeno biológico que refleja las restricciones que la heterogeneidad de paisaje impone, las cuales a su vez podrían tener un potencial efecto sobre las conductas de forrajeo (Johnson et al. 1992a, Wiens et al. 1993a, 1997). Una forma de estudiar la conducta de desplazamiento es el análisis de las vías de movimiento, las cuales corresponden a la trayectoria espacial de un individuo de una localidad a otra durante un período de tiempo específico (Turchin et al. 1991). Estas vías se caracterizan por presentar una dirección media, y una distribución de ángulos de giro y distancias de desplazamiento (Wiens et al. 1993b), las cuales proveen de un registro de cómo los organismos perciben e interactúan con la heterogeneidad espacial (Kotliar & Wiens 1990, With 1994a). Este tipo de mediciones constituye en sí mismo una aproximación simple y descriptiva acerca del tipo de trayectoria exhibida por un organismo, y es posible predecir que una vía de movimiento compleja debiera implicar una mayor longitud de desplazamiento, un alto número de giros (e.g. ángulos superiores a 45°) y no presentar una orientación definida. Además, las vías de movimiento han sido

Kacelnik & Houston 1984). El MFLC al involucrar distancias entre un lugar central y el parche de recursos (Orians & Pearson 1979, Schoener 1979), permite estudiar experimentalmente restricciones que la heterogeneidad espacial de la matriz impone sobre el transporte de alimento y las trayectorias de los organismos. Por otra parte, la relevancia de incorporar el procesamiento de información realizado por los individuos en la teoría de forrajeo óptimo, ha sido discutida y sugerida en trabajos de ecología de paisaje, pero se carece de estudios que aborden el tema en forma explícita (e.g. Wiens et al. 1993a, Ims 1995).

Heterogeneidad espacial de paisaje y procesamiento de información.-

La heterogeneidad espacial es una característica fácil de observar, sin embargo, ha sido difícil de definir y medir con precisión (Forman & Godron 1986, Li & Reynolds 1994). La heterogeneidad ha sido tradicionalmente entendida como la composición de partes de diferente clase en el ambiente, es decir, es considerada una expresión medible de la variabilidad espacial sobre la totalidad de un área (Kolasa & Rollo 1991, Wiens 1995). Por tanto, heterogeneidad (varianza espacial > 0) y homogeneidad (varianza espacial = 0) constituyen conceptos contrastantes en un sentido estadístico (Wiens 1995). En estos términos, la heterogeneidad espacial corresponde a una característica estructural de los sistemas ecológicos (McIntosh 1991, Bell et al. 1993, Li & Reynolds 1994).

Una definición operacional de heterogeneidad sugerida por Forman (1995), corresponde a la distribución desigual de objetos en el espacio. Algunos índices estiman la disposición de obstáculos en un paisaje, en los cuáles se evalúa la distancia promedio entre objetos vecinos y la densidad promedio de éstos (e.g. "índice de dispersión de parches", véase Forman & Godron 1986, Forman 1995). Por tanto, este tipo de índices destaca atributos que están relacionados con la configuración y arreglo espacial de un mosaico de objetos (Li & Reynolds 1994). De este modo, si consideramos una densidad constante de objetos que imponen restricción al movimiento de los organismos, entonces es posible proponer como una "medida de heterogeneidad" (*sensu* Kolasa & Rollo 1991, With 1994b) cuatro paisajes en orden decreciente de homogeneidad espacial: sin estudiadas mediante ajustes a simulaciones y/o modelos matemáticos como la difusión y el caminar azaroso (Kareiva & Shigesada 1983, McCulloch & Cain 1989, Bell 1991, Johnson et al. 1992b), así como por medio de una medida escala-independiente conocida como la dimensión fractal (With 1994b, Wiens et al. 1995; pero véase Turchin 1996, 1998).

Las conductas de alimentación de los organismos han sido formalizadas en un cuerpo teórico conocido como teoría de forrajeo (Stephens & Krebs 1986, Perry & Pianka 1997). Desde su formulación esta teoría ha considerado la naturaleza heterogénea (i.e. parchosa) de la distribución de recursos en el ambiente, y ha analizado la implicancia de ésta en el comportamiento trófico de organismos que optimizan la ganancia de energía (i.e. maximizan la energía ingerida) e inversión de tiempo (i.e. minimizan los tiempos de viaje y explotación) (MacArthur & Pianka 1966, Emlem 1966, Schoener 1971, Charnov 1976). El modelo de forrajeo en lugar central (MFLC), un caso particular del modelo de uso de parches, consiste en que las presas capturadas por un individuo son transportadas a un lugar central fijo (e.g. nido) donde son consumidas, almacenadas o sirven de alimento para sus crías (Orians & Pearson 1979, Schoener 1979, Pyke 1984, Stephens & Krebs 1986). Durante esta actividad existe gasto de energía en los viajes de ida y vuelta así como en la manipulación de presas, existiendo adquisición de energía sólo durante el período de ingesta (Orians & Pearson 1979). Se han analizado los efectos del tamaño de carga transportado, y tiempos de residencia involucrados en el MFLC (Giraldeu & Kramer 1982, Kacelnik 1984, Houston & McNamara 1985, Kacelnik et al. 1986, Wetterer 1989). Las decisiones de un organismo que se aleja de su lugar central en búsqueda de alimento deben apuntar a maximizar la entrada de energía para de esta forma incrementar su adecuación biológica (Orians & Pearson 1979). Así, a medida que incrementa la distancia, y por ende el tiempo de travesía, entre un parche de recursos y un nido, se generan las siguientes predicciones generales: i) los organismos seleccionarán presas más grandes en tamaño y/o más ricas en energía, y ii) los organismos incrementarán el tiempo de permanencia en el parche. Estas predicciones, sin embargo, no han tratado en profundidad los costos energéticos y la inversión de tiempo en que incurren los forrajeadores (Schoener 1979, obstáculos < objetos distribuidos uniformemente < objetos distribuidos al azar < objetos con distribución agrupada.

La transmisión de información es un procedimiento mediante el cual una entidad (el emisor) afecta a otra (el receptor) mediante el traspaso de señales y su posterior transformación en mensajes, período en el cual la acción ejecutada por el emisor se vuelve más predecible para el receptor (Shannon & Weaver 1949, Halliday 1983, Dusenbery 1992, Bradbury & Vehrencamp 1998). Es decir, el uso de información es un proceso asociado con la reducción en incerteza en el desempeño de una conducta por parte de un receptor (Lieberman 1993, Stephens 1993). En el contexto de esta tesis, el interés esta puesto en analizar ¿cuán efectivamente el mensaje recibido afecta la conducta en la manera esperada? (i.e., el problema de efectividad de la comunicación, *sensu* Shannon & Weaver 1949). Esta es una aproximación útil para determinar cuándo y en qué cantidad, el comportamiento de un animal está determinado por su experiencia de relación con el medio ambiente abiótico y/o por la interacción con otros organismos (Harper 1991).

Los modelos de difusión y caminar azaroso consideran a los individuos como entidades "sin información" respecto a las decisiones y conductas de desplazamiento (Ims 1995, Lima & Zollner 1996). En el otro extremo, uno de los supuestos básicos de los modelos clásicos de forrajeo óptimo afirma que los animales tienen información completa acerca de las características del ambiente (e.g. los animales conocen los tipos de parches y presas, Stephens & Krebs 1986). Sin embargo, los animales no son ni omniscientes ni carentes de información respecto a los atributos de un medio externo incierto y cambiante; pueden modificar sus conductas de alimentación vía acumulo de experiencia (memoria) y/o aprendizaje acerca de la distribución, abundancia y/o calidad de los recursos tróficos, lo cual se traduce finalmente en cambios en los tiempos de búsqueda y permanencia en los parches (McNamara & Houston 1985, 1987, Lieberman 1993, Stephens 1993). Respecto a la presencia de recursos novedosos en un ambiente heterogéneo, los organismos experimentan a lo largo de una secuencia temporal: i) eventos de adquisición de información, que dicen relación al grano de percepción de los organismos, y ii) uso de esta información, lo que se traduce en incrementos en el desempeño de alguna actividad por parte de los individuos (Giraldeau 1997, Rodríguez-Gironés & Vásquez 1997, Dukas 1998, Ydenberg 1998).

Complejidad de movimiento y eficiencia de forrajeo.-

En la literatura está bien documentado que la estructura del hábitat restringe las trayectorias de los individuos debido a las barreras físicas que éste impone a sus movimientos (Johnson et al. 1992a, Ims 1995, McIntyre & Wiens 1999, With et al. 1999, Zollner & Lima 1999). Se ha encontrado que paisajes homogéneos y con pocos obstáculos generan un patrón de movimiento lineal en diferentes tipos de organismos. En cambio, ambientes heterogéneos determinan que los animales exhiban trayectorias más sinuosas, es decir, con una gran sobreposición y área cubierta (With 1994a, Wiens et al. 1995). Sin embargo, estos estudios no han especificado: i) el estímulo (e.g. alimento, pareja reproductiva, depredadores) que desencadena los desplazamientos, ii) el cambio en complejidad que las trayectorias individuales experimentan en el tiempo como resultado de la adquisición de información desde el ambiente (e.g. marcas familiares del paisaje, tasas de contacto corporal), y iii) el efecto que tendría el desempeño locomotor sobre la ejecución de otras conductas (e.g. éxito de forrajeo).

Respecto a las conductas de alimentación, los modelos de forrajeo óptimo no han considerado explícitamente la complejidad de movimiento exhibida por los organismos en la matriz entre parches de alimento (véase e.g., Charnov 1976, Pyke 1984). La problemática del movimiento de los individuos sólo ha sido abordada al interior de cada parche de recursos tróficos. Así, el supuesto de "búsqueda azarosa de alimento" analiza su efecto sobre la disminución de los recursos en el tiempo (Charnov et al. 1976, Stephens & Krebs 1986); y el supuesto de "búsqueda concentrada en un área" explicita que cuando un organismo encuentra un recurso, éste reorienta su búsqueda a una región más circunscrita debido a procesos de adquisición y uso de información (Stillman & Sutherland 1990, Benhamou 1992, Krakauer & Rodríguez-Gironés 1995). De esta forma, no existen estudios que evalúen cómo trayectorias con distinta geometría tienen efecto sobre la ganancia de energía (b_i) y el costo de energía (c_i) durante el forrajeo. Las vías de movimiento que involucran un mayor retorno energético constituirían una característica clave para el organismo que las exhibe, pues implicarían un incremento en su adecuación biológica. De hecho, se ha documentado en micromamíferos y aves que un aumento de la tasa de entrada de energía se traduce en una mayor sobrevivencia y reproducción de los individuos (e.g. Ritchie 1990, Lemon 1991). La teoría de forrajeo ha considerado varias variables que maximizarían la adecuación biológica de los organismos durante sus actividades de alimentación. Entre éstas se encuentran la tasa bruta (b_i), la tasa neta ($b_i - c_i$), y la eficiencia de forrajeo (b_i/c_i) (Ydenberg et al. 1994, Houston 1995, Bautista et al. 1998). En estudios de campo, una variable frecuentemente utilizada es la razón entre número de presas capturadas (n) / unidad de tiempo invertido (t), conocida como la tasa de remoción de recursos. Cabe esperar que si los individuos maximizan este cuociente obtendrán un valor más alto en adecuación biológica. En esta tesis se evaluó esta última variable como un estimador del éxito de forrajeo de los organismos.

En el esquema de la Fig. 1 establezco las siguientes relaciones causales: (1) Una mayor heterogeneidad espacial producirá un decremento en el desempeño locomotor de los organismos. Además, en esta tesis focalizo la atención en el recurso alimento (el cual constituye parte de la heterogeneidad espacial de paisaje) como el estímulo que genera los desplazamientos de los organismos. Específicamente, se analizan las trayectorias de retorno de los animales que transportan una carga de alimento hacia el lugar central (e.g. nido). (2) Sin embargo, las conductas de movimiento no son una fotografía sino una película que cambia con el transcurso del tiempo. Así, a medida que un individuo adquiere información desde su entorno se producirá una mejora en la ejecución de sus trayectorias. (3) Vías de movimiento más eficientes (e.g. menor longitud de desplazamiento, menor tiempo de viaje, mayor velocidad de locomoción) se traducirán en un incremento del éxito de forrajeo (e.g. mayor tasa de remoción de recursos). Con el objetivo de evaluar la generalidad de estas relaciones, es interesante estudiar dentro de un grupo de organismos (e.g. hormigas) diferentes especies en las que se analice el efecto de: la heterogeneidad de paisaje a distintas escalas espaciales (e.g. centímetros, metros), diferentes tipos de hábitos tróficos (e.g. generalistas, especialistas), y distintas modalidades de explotación de un parche de recursos (e.g. individual, grupal).

En general, el desempeño locomotor y de alimentación en un mosaico de parches han sido tratadas como conductas independientes entre sí (e.g. Charnov 1976, With 1994a, Krakauer & Rodríguez-Gironés 1995, Wiens et al. 1995). En este contexto, el esquema de la Fig. 1 que representa la problemática conceptual abordada en esta tesis, es particularmente novedoso por cuanto no existen trabajos previos en los cuales se haya analizado la existencia de una relación causal entre complejidad de movimiento y éxito de forrajeo de los organismos modulada por la heterogeneidad espacial del paisaje y el procesamiento de información. De esta forma, el esquema de la Fig. 1 constituye un modelo inicial simple respecto del establecimiento de relaciones entre estos factores. Específicamente, la aceptación, modificación o rechazo de este modelo es abordado en el capítulo 1, y sus implicancias son discutidas en la conclusión general de esta tesis. En particular, el establecimiento de la relación entre locomoción y forrajeo, permitirá evaluar si los individuos exhiben distintas estrategias conductuales de movimiento y forrajeo dependiendo de las situaciones ambientales (espaciales y temporales) a las cuales se ven confrontados. Hasta la fecha no se han realizado este tipo de estudios. La presente tesis pretende hacer un aporte en este sentido.

Las hormigas como modelo de estudio.-

Las hormigas en comparación a otros insectos (e.g. coleópteros, ortópteros) presentan trayectorias complejas, lo cual sugiere que perciben el hábitat en forma de grano grueso o con "sensibilidad de parche" mientras buscan y manipulan recursos tróficos (*sensu* Kotliar & Wiens 1990, Wiens et al. 1995, Kaspari & Weiser 1999). Se ha documentado que los himenópteros sociales son forrajeadores de lugar central durante todo su ciclo de vida, y se les considera organismos transportadores de una sola carga de alimento a la vez (Harkness & Maroudas 1985, Bailey & Polis 1987, Hölldobler & Wilson 1990). El pequeño tamaño corporal que presentan los formícidos (e.g. en relación a vertebrados) permite que en arenas experimentales reducidas se puedan generar diseños y tratamientos que analicen el efecto de distintos factores espaciales sobre las conductas de locomoción y alimentación. Estos atributos convierten a las hormigas en un buen sujeto de estudio para abordar la problemática de esta tesis.

Conductas de movimiento.- Algunas especies de hormigas cuando exploran el ambiente pueden hacerlo en línea recta o a través de desplazamientos sinuosos (Harkness & Maroudas 1985, Leonard & Herbers 1986, Gordon 1994). Estos patrones de movimiento constituyen estrategias de navegación espacial que permiten buscar alimento y evitar obstáculos en el espacio (Collet 1996). De esta forma, características estructurales del substrato (e.g. cobertura de herbáceas), factores abióticos (e.g. temperatura), y la distribución en parche de los recursos (e.g. semillas), restringen las vías de movimiento y afectan el forrajeo de las hormigas (Crist & MacMahon 1991, Crist & Haefner 1994, Crist & Weins 1994). Las vías de movimiento con ángulos de giro erráticos y una gran sobreposición de recorridos, incrementan el área explorada y la probabilidad de que una obrera descubra nuevos items de alimento (Hölldobler & Wilson 1990, Schweitzer et al. 1997). De esta forma, los individuos integran los errores de sus trayectorias y así incrementan la eficiencia de búsqueda y explotación de recursos durante el forrajeo (Deneubourg et al. 1983, Hölldobler & Wilson 1990). De hecho, las hormigas mientras buscan alimento, se mueven en forma compleja y a una baja velocidad, en cambio, una vez que han capturado sus presas e inician su retorno al nido, éstas se mueven más linealmente y a una mayor velocidad (Leonard & Herbers 1986, Johnson 1991, Herbers & Choiniere 1996).

Las hormigas adquieren información acerca de las características físicas del ambiente mientras se desplazan. Así por ejemplo, mediante el uso del sistema visual una obrera es capaz de reconocer marcas familiares existentes en el paisaje (e.g. ubicación relativa del nido, piedras, arbustos) y/o señales en el cielo (e.g. posición del sol, patrón de luz polarizada) (Wehner 1996, Collet et al. 1998, Nicholson et al. 1999, Schatz et al. 1999). Por otra parte, la producción de señales químicas como las feromonas de camino ("trail pheromones") permite la transmisión de información entre obreras sobre la ubicación y calidad de los recursos, lo cual determina el reclutamiento y orientación hacia la fuente de alimento, y modula la forma de sus trayectorias de forrajeo (Hölldobler & Wilson 1990, Gordon 1994, Sumpter & Beekman 2003).

Conductas de alimentación.- Las conductas de forrajeo en hormigas varían entre especies con obreras que en forma individual buscan y transportan alimento hacia el nido, y aquellas que realizan estas actividades en grupos (Carroll & Janzen 1973, Oster & Wilson 1978, Herbers 1981, Hölldobler & Wilson 1990). Este último comportamiento de alimentación involucra una diversidad de estrategias cooperativas entre los individuos, las cuáles dependen de la variabilidad espacio-temporal en la distribución y abundancia del alimento (Traniello 1989, Fewell 1990, López et al. 1994). Algunos estudios en hormigas han apoyado la predicción del MFLC en cuanto a que a mayor distancia recorrida entre el nido y sitio de alimentación, incrementa el nivel de selectividad por presas más ricas en energía y/o más grandes en tamaño (Rissing & Pollock 1984, Schmid-Hempel 1984, Crist & MacMahon 1992, Roces & Nuñez 1993). Sin embargo, otros trabajos han resaltado que durante el desempeño de tareas de forrajeo lo relevante para las obreras es minimizar el tiempo invertido durante las travesías de búsqueda, manipulación y transporte del alimento (Fewell 1988, Weier & Feener 1995).

Una explotación eficiente de los recursos, requiere que las hormigas comuniquen información sobre nuevas fuentes de alimento a otras compañeras de nido y así se genere un trabajo colectivo que incremente el desempeño de forrajeo de la colonia (Adler & Gordon 1992, Roces & Nuñez 1993, Haefner & Crist 1994). Existen diversos mecanismos (e.g. señales vibratorias, marcas químicas, tasas de encuentro) que permiten a las hormigas comunicar este tipo de información (Hölldobler & Wilson 1990, Gordon et al. 1993, Hölldobler 1995). Así por ejemplo, las tasas de contacto corporal y/o antenal entre obreras patrulleras y forrajeadoras permite reclutar un gran número de individuos en actividades de colecta de alimento (Gordon 1987, Adler & Gordon 1992, Gordon 1994). Este proceso parece estar gobernado por reglas simples de decisión ("rules of thumb"); es decir, si una obrera en un determinado trayecto y lapso de tiempo supera un valor umbral de encuentros con hormigas que ejecutan una determinada función (e.g. acarreo de alimento), este individuo se abocará a la realización de esta tarea (Gordon 1989, Gordon et al. 1993). En esta toma de decisiones subyacen mecanismos químicos (e.g. secreción de hidrocarburos de cutícula) que permiten a una obrera reconocer el tipo de tarea desempeñada por una compañera de colonia (e.g. Wagner et al. 1998, 2000, Greene & Gordon 2003).

La colonia de hormigas.- Las conductas de desplazamiento y alimentación de las obreras son el reflejo de interacciones que emergen de un nivel de organización superior, la colonia de hormigas (Traniello 1989, Gordon 1996, Herbers & Choiniere 1996). Una colonia puede ser entendida como un superorganismo, en términos de su organización jerárquica, comunicación interna, e interacción con su medio externo (Seeley 1989, Wilson & Sober 1989, Hölldobler & Wilson 1990). Se ha determinado que el rango y direccionalidad de las rutas de forrajeo en hormigas, son sensibles a la edad, tamaño, medio social interno (e.g. estado de actividad de los individuos) e historia social de la colonia (e.g. escasez de reservas) (Wilson 1985, Houston et al. 1988, Gordon 1991, 1995, 1999). De esta forma, la complejidad de movimientos exhibidos por los individuos y la colonia en su conjunto puede ser analizada mediante el "mapeo" de las formas irregulares (e.g. en forma de pseudopodios) que adopta su territorio de forrajeo, y la eficiencia de alimentación puede ser estimada al considerar el total de alimento removido en un lapso determinado de tiempo (i.e. tasa de remoción de recursos).

Objetivo general.-

El objetivo general de esta tesis fue determinar el efecto de la heterogeneidad espacial de paisaje y uso de información sobre la relación entre desempeño locomotor y éxito de forrajeo en especies de hormigas que presentan diferentes escalas espaciales de desplazamiento, hábitos tróficos, y modalidades de explotar un parche de recursos.

Objetivos específicos.-

- Determinar el efecto de la heterogeneidad de hábitat sobre el desempeño locomotor en organismos forrajeadores de lugar central.
- Determinar el efecto de la adquisición de información sobre las vías de movimiento individuales.
- Determinar la relación entre desempeño locomotor y éxito de forrajeo en colonias de hormigas.

Hipótesis de trabajo.-

Respecto a individuos que están constantemente desplazándose entre un lugar central y parches de recursos tróficos (véase problemática de esta tesis en Fig. 1), a continuación se formulan las siguientes hipótesis y predicciones acerca de conductas de movimiento y forrajeo que operan a nivel del organismo:

Hipótesis 1: En comparación a un paisaje homogéneo, en un paisaje heterogéneo los organismos presentarán un bajo desempeño locomotor y una menor tasa de remoción de recursos debido a que la estructura física del hábitat impone mayores restricciones de desplazamiento y percepción.

Predicción 1: A medida que la distribución de obstáculos en el espacio presenta una mayor heterogeneidad, aumenta la complejidad de los movimientos y disminuye el éxito de forrajeo de los individuos (Fig. 2a).

Hipótesis 2: Durante el transcurso del tiempo en que un nuevo parche de alimentos empieza a ser explotado, los organismos experimentarán una transición desde menor a mayor desempeño locomotor y un incremento en la tasa de remoción de recursos debido a que éstos adquieren y usan información desde su ambiente.

Predicción 2: A medida que incrementa la información sobre la ubicación y calidad de un nuevo parche de recursos, disminuye la complejidad de los movimientos y aumenta el éxito de forrajeo de los individuos (Fig. 2b).

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Leyenda de Figuras

Figura 1: Modulación ejercida por la heterogeneidad espacial de paisaje y la adquisición de información, sobre la relación causal entre desempeño locomotor y éxito de forrajeo de los organismos. Las flechas de línea continua representan aspectos bien documentados en la literatura, y las flechas de línea punteada constituyen las relaciones escasa o nulamente analizadas en estudios previos, y que son el tema central de esta tesis (véase texto para más detalles).

Figura 2: Efectos hipotéticos de la heterogeneidad espacial de paisaje (**a**) y adquisición de información (**b**), sobre la complejidad de movimiento y éxito de forrajeo de los organismos. Se asumen relaciones lineales, para facilitar la comprensión del efecto de ambos factores sobre las variables respuestas.

Figura 1

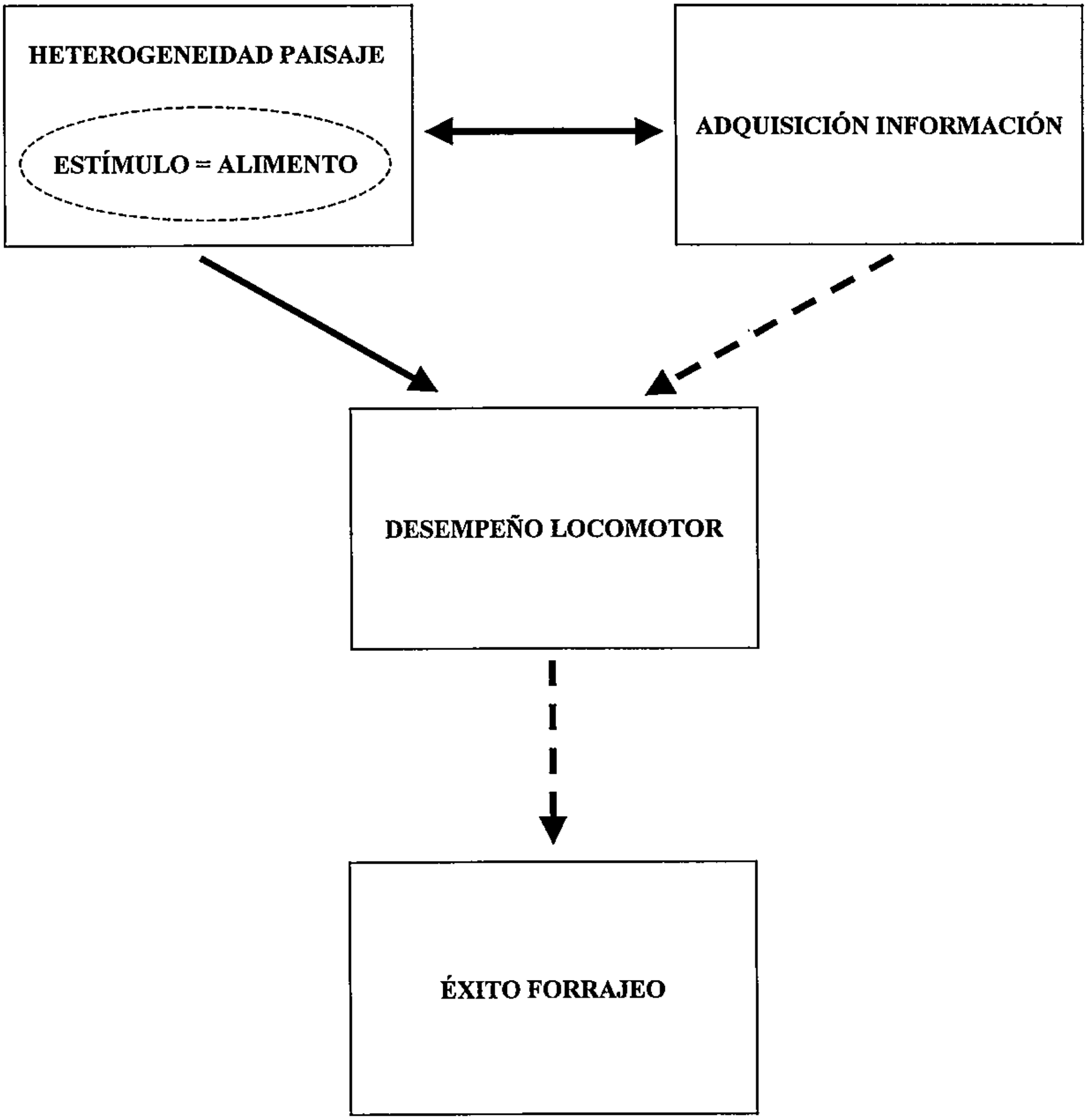
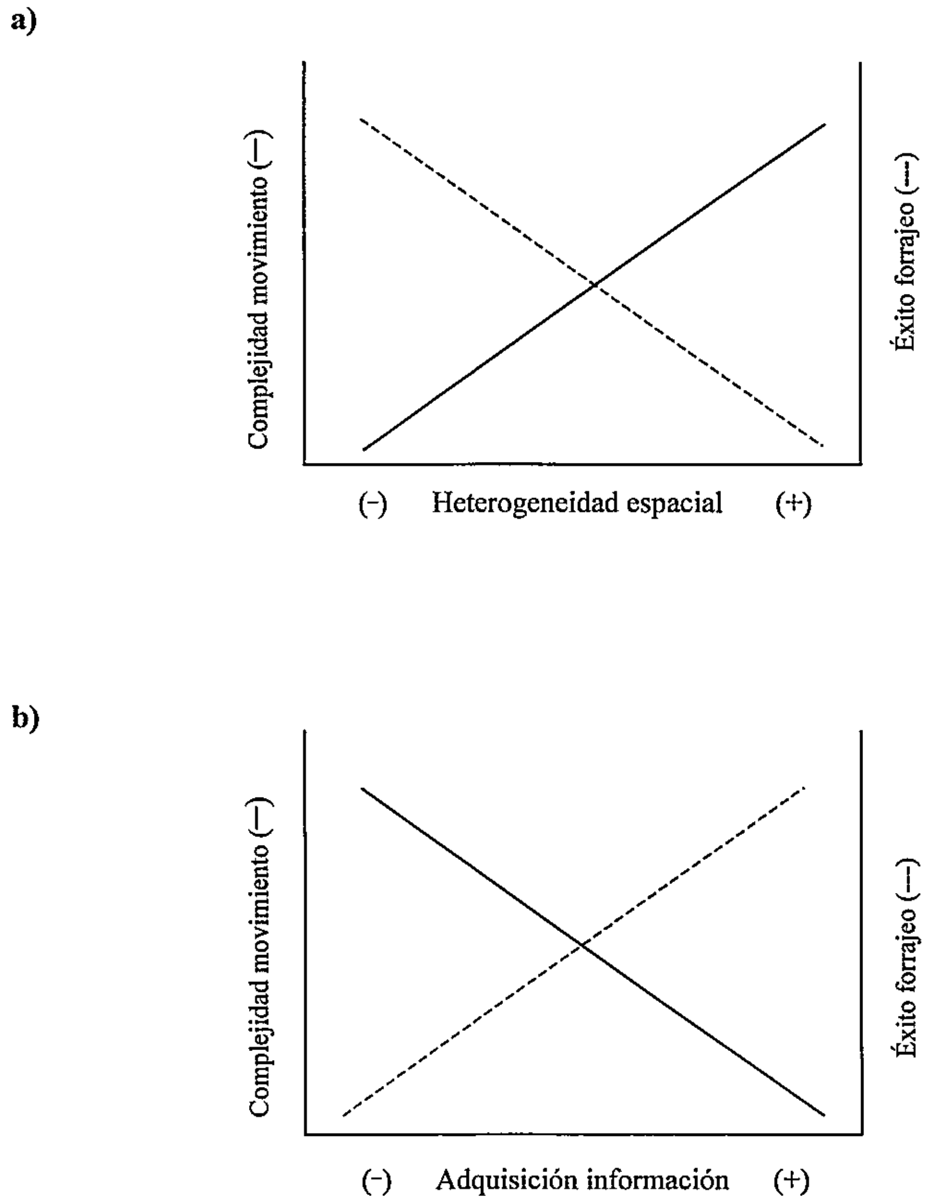

HETEROGENEIDAD PAISAJE
ESTÍMULO = ALIMENTO
ADQUISICIÓN INFORMACIÓN
DESEMPEÑO LOCOMOTOR
ÉXITO FORRAJEO

Figura 2


a)
Complejidad movimiento (—)
Éxito forrajeo (---)
(-) Heterogeneidad espacial (+)
b)
Complejidad movimiento (—)
Éxito forrajeo (---)
(-) Adquisición información (+)

CAPÍTULO 1

Foraging performance in ants: the role of substratum heterogeneity, movement complexity and information acquisition

ABSTRACT

Locomotion and foraging behaviors are performed in heterogeneous habitats, and are dependent on the information acquired by individuals from their environment. Traditionally, locomotion and foraging behavior have been studied as independent events in the literature. Landscape ecology has studied the effects of spatial heterogeneity on the complexity of movement paths, but has not specified the stimulus that triggers movement, the changes in complexity that trajectories experience through time as result of information accumulation, nor the influence of locomotion performance on foraging behavior. On the other hand, models of optimal foraging have not considered explicitly the complexity of movement displayed by organisms in the matrix between food patches, and, therefore, they have not been analyzed the consequences on feeding performance. These relationships were studied in the species *Dorymyrmex goetschi* (subfamily Dolichoderinae), a harvester ant that inhabits semiarid and mediterranean environments. In a lower Andes locality of central Chile I selected 30 nests of *D. goetschi*, and offered a food patch located to different distances from the nest entrance. Substratum heterogeneity was estimated as the proportion of ground surface covered by physical elements that restrict ant locomotion. I video recorded the behavior of each colony and analyzed the following variables: the number of active foragers, the number of head contacts per capita per trip (a mechanism of information transfer), the path length used by workers to transport a food load from the resource patch to the nest (a measure of movement complexity), the number of captured prey by colony, and the duration of patch exploitation. In food patches located at a greater distance from colonies, the maximum number of foragers is reached earlier. There was a positive and significant relationship between the number of foragers and the number of head to head contacts. During the initial phase of exploitation, path length was significantly longer. In food patches located at greater distance, the amount of captured prey was significantly lower, the time invested in patch exploitation was greater, and the removal rate was lower. A path analysis showed that the spatial heterogeneity and movement complexity had a negative, but not significant effect on foraging success. However, information acquisition had a positive and significant direct effect on resource removal rate. The dissemination of information between the workers about the location and quality of a new food patch, structural characteristics of the habitat, and mortality risks, can affect displacement, recruitment and collective work of a colony, determining the efficiency whereupon resources are exploited.

Key words: landscape, head contact, ant colonies, patch distance, path length, resources removal rate.

INTRODUCTION

Locomotion and foraging are important behaviors with potential fitness consequences for animals. Locomotion allows, for example, search of refuges and reproductive pairs, and feeding allows satisfying the energetic and nutritional demands of the individuals (Bell 1990, Wehner 1997). Generally, animals perform these activities in heterogeneous habitats with patchy distribution and abundance of resources, microclimatic conditions, competitors, predators, vegetation structure and abiotic elements (Southwood 1977, Kolasa & Rollo 1991, Kozakiewicz 1995). Besides, the level of perceptual resolution during the displacements of the individuals restricts the type of spatial heterogeneity to which they are confronted (Allen & Hoekstra 1991, Zollner & Lima 1997).

In the literature is well documented that habitat structure restricts the trajectories followed by the animals due to physical barriers that constraint movement (Ims 1995, McIntyre & Wiens 1999, With et al. 1999, Zollner & Lima 1999). Generally, homogenous landscapes with few obstacles generate patterns of linear movement paths in different types of animals, while heterogeneous environments determine more sinuous trajectories, that is, with a higher superimposition of paths and a higher covered area (With 1994, Wiens et al. 1995). Nevertheless, these patterns up to date have not been linked sufficiently to: (1) the stimulus that trigger movements, (2) the changes in complexity that the individual trajectories experience through time as result of information accumulation, and (3) the influence that locomotion performance can have on foraging behavior. Models of optimal foraging have not considered explicitly the movement complexity displayed by the organisms in the matrix between patches (Charnov 1976, Pyke 1984). The problem of individual movement has only been analyzed inside food patches. Thus, the assumption of "random search" has been used to analyze the decrease of resources through time (Charnov et al. 1976, Stephens & Krebs 1986), and the assumption of "area-concentrated search" asserts that when an organism finds a resource, reallocate its searching effort to a more restricted region (Stillman & Sutherland 1990, Benhamou 1992). The model of central place foraging, a particular case of the patch use model, consists in that prey captured by an individual are transported to a fixed central place (e.g. nest) where they are consumed, stored or serve as food for its young (Orians & Pearson 1979, Schoener 1979, Pyke 1984, Stephens & Krebs 1986). Thus, this model involves the distance between, for example, a nest and resource patches (Orians & Pearson 1979, Schoener 1979), which allows to study experimentally the effects that the spatial heterogeneity of the matrix and the information use have on food transport and the trajectory of foragers (e.g. Ydenberg 1998).

In general, locomotion performance and feeding success in a mosaic of patches have been treated as independent events (e.g. Charnov 1976, Krakauer & Rodríguez-Gironés 1995). In this work I studied the effects of landscape spatial heterogeneity and information acquisition on movement complexity, and analyzed how locomotion performance influences foraging success of a social insect. I predicted that greater spatial heterogeneity will decrease locomotion performance of organisms. Nevertheless, movement can be improved through time as individuals are acquiring information from their environment. Thus, I predict that movement path will become shorter (e.g. shorter path length) through time, which in turn will increase foraging success (e.g. greater resource removal rate) of foragers.

Ants are good subjects for studying foraging ecology because they present a series of attributes amenable for experimental research. Forager workers exhibit high variability in their trajectories (Leonard & Herbers 1986, Gordon 1994), which are affected by structural characteristics of the substratum and spatial distribution of resources (Crist & MacMahon 1991, Crist & Haefner 1994, Crist & Weins 1994). Ants are central place foragers that transport single food loads (Harkness & Maroudas 1985, Bailey & Polis 1987, Hölldobler & Wilson 1990), thus, during their travels workers acquire information about the physical characteristics of the habitat and the quality of novel resources. Several mechanisms have been demonstrated by which ants communicate this type of information to conspecifics (Hölldobler & Wilson 1990, Gordon et al. 1993, Hölldobler 1995). For example, the rates of antennal contacts between workers scouts and foragers allow recruitment of a large number of individuals

(Gordon 1987, Adler & Gordon 1992, Gordon 1994). This process operates apparently by way of simple decision rules (rules of thumb), that is, if a worker at a certain distance and during a certain time interval surpasses a threshold value of encounters with other ants performing a given task (e.g. food transportation), this individual will joint this activity (Gordon1989, Gordon et al. 1993). Finally, the small body size of these animals allows that in landscapes of a few square meters it is possible to evaluate the effect of spatial heterogeneity on the behavior of interest.

The aim of this study was to evaluate the influence of movement paths on exploitation performance of a novel food patch in ants that are constantly confronting a given landscape spatial heterogeneity and using information. Specifically, I asked the following questions. (1) What effects produce substratum with different spatial heterogeneities on resource removal rate? (2) Is there a causal relationship between locomotion and foraging performance? (3) What changes produce encounters among individuals on feeding activities? I predict that: (i) landscapes with more physical barriers reduce foraging performance, (ii) more linear movements increase prey removal rate, and, (iii) a greater number of contacts per capita among nestmates increases foraging success. Data are discussed in relation to the theory of central place foraging and information processing in social insects.

MATERIALS AND METHODS

Study site and species

The fieldwork was conducted in the Rio Clarillo National Reserve (33° 51' S, 70° 29' W), a lower Andes locality of central Chile located 45 km SE from Santiago. Vegetation is composed mainly by evergreen sclerophyllous woody plants, and annual and perennial herbs (Gajardo 1993). The climate has a cold temperate regime with precipitations concentrated during the winter and a dry hot period of about seven months around summer.

The studied species, *Dorymyrmex goetschi* Menozzi 1935, belong to the subfamily Dolichoderinae (Snelling & Hunt 1975, Shattuck 1992). The workers of this species have red coloration in head and thorax, a black abdomen, and a mean body mass of about 1.6 mg (Torres-Contreras & Vásquez 2004). These ants construct their nests in open spaces without tree or shrub vegetation cover. The entrance of nests have characteristic earth hillocks produced by rubble removed from the interior by the ants. Activity of ants begins at dawn with a period of nest cleaning, followed by a period of exploratory and foraging activities. These activities are performed until soil temperature reaches 45° C. At this temperature the entrance of the nest is closed with vegetable material and activities cease above ground (H. Torres-Contreras, *personal observation*). This species has been documented as belonging to the assembly of harvester ants (Medel & Vásquez 1994, Torres-Contreras 2001). Analysis of natural prey transported to the nest shows that this species predate on insects with a frecuency of 27-47 % (H. Torres-Contreras, *unpublished data*). *Dorymyrmex goetschi* constitutes together with *Camponotus chilensis* and *C. morosus*, one of the most common ant species present in the study site (H. Torres-Contreras, *personal observation*).

Experimental design

The fieldwork was carried out between late October and early December 2001 during the spring season. In the field, *D. goetschi* transport natural loads with a mean mass of 0.97 ± 0.07 mg (mean ± SE, n= 506, range 0.002 - 13.542 mg, Torres-Contreras & Vásquez 2004). I used compacted sugar microspheres (5.61 ± 0.05 mg, mean ± SE, n= 100) commercially available as experimental prey. Although the size of experimental food items was in the upper range of the natural prey size distribution of this species, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey size variability was low or nil. Further, my observations revealed that prey handling did not vary with these food items. I selected 30 nests of *D. goetschi* to which we offered a food patch of 100 microspheres. To 10 colonies selected at random we placed the food patch at a distance of 10 cm from the nest entrance, to 10 colonies the patch was located at a distance of 20 cm, and to the other 10 colonies the resource patch was located at a distance of 40 cm from the nest opening. These distances were within the normal foraging range of this species (i.e., 0.0-2.0 m; H. Torres-Contreras, *personal observation*). Resource patches were set at 8:00 AM and I video recorded (Sony camera, model CCD-TR818) the movement and feeding behavior of forager workers until the resource was depleted and/or the activity stopped. Videos were watched and the following variables were measured: number of active foragers, number of head contacts per capita per trip, number of captured prey by colony, and duration of patch exploitation. I also drew the trajectories of workers that transported one food load (one microsphere in all cases) from the patch to the nest to assess movement path length.

Landscape spatial heterogeneity was estimated with linear transects that were arranged through the matrix that separated the entrance of the nest and the food patch. Following Johnson et al. (1992), I calculated a heterogeneity index that considers the proportion of ground surface covered by physical elements that could inhibit ant locomotion (e.g., stones, twigs, leaves, and/or grass; 2 mm width and length, or larger), in relation to the total surface that include bare ground. For example, if 1 cm is covered by twigs and 2 cm by grass, out of a total distance of 10 cm, then the heterogeneity index has a value of 0.3. The heterogeneity index was of 0.39 ± 0.11 (mean ± SE, n = 10, range 0.00-0.87) for distances of 10 cm, 0.11 ± 0.05 (range 0.00-0.43) for 20 cm, and 0.48 ± 0.09 (range 0.05-0.90) for 40 cm. The relationship between distance and heterogeneity was not significant ($r^2 = 0.016$, $t = 0.656$, $p = 0.517$).

A high density of individuals has been correlated with increases in the antennal contact rates per ant (e.g. Gordon 1996), and with decision making through chemical mechanisms of recognition (e.g. Greene & Gordon 2003). In this study, I quantified minute by minute the number of foragers present in the matrix between the food patch and nest opening, and the number of brief head to head contacts that each worker experienced in their inbound trips (patch to nest) was used as an estimate of information transfer. I followed the methodology and criterion used by Gordon et al. (1993) and Burd & Aranwela (2003) to determine an effective contact between two ants.

Movements of individuals between the food patch and the nest were traced in transparent films put directly over a video monitor. These trajectories were scanned and converted to digital images. Path lengths were measured by using SigmaScan software (SPSS Inc.). This measurement is a simple description of the movement complexity exhibited by an organism (e.g. Turchin et al. 1991). I estimated a route index as the ratio between path length and distance in straight line from patch to the nest (Dejean & Benhamou 1993, using a similar index). I quantified, minute by minute, the number of sugar microspheres captured by the colony, and considered a successful removal when a prey was introduced to the nest by a worker. The duration of patch exploitation was estimated as the time taken by a colony to remove 100% of resources or until activity stopped. For analysis, the exploitation time was divided in three phases (initial, half, final) with the objetive of evaluating changes in the feeding performance through time. The foraging performance at the colony level was evaluated by means of total resource removal rate (i.e. number of captured prey / minutes invested in patch exploitation).

Statistical analysis

The effect of exploitation time (phase), patch distance, and the interaction between both factors on the number of active foragers and the route index was analyzed with a two-way ANOVA, with colony used as covariate. Simple linear regressions were used to analyze the relationships between number of active foragers and number of head contacts per trip. A one-way ANOVA was carried out to evaluate the effect of patch distance on the number of prey captured, time of patch exploitation, and resource removal rate. Colony was used as the sample unit, and hence data correspond to the mean of foragers per colony (the range of the number of workers for 10 cm distance was of 7-14; for 20 cm distance was of 3-14, and for 40 cm distance was of 2-14). All tests were carried out with Statistica 6.0 software (StatSoft Inc.). Data shown correspond to the mean ± one standard error, and the significance of the statistical tests was fixed to $\alpha = 0.05$. Data satisfied the assumptions of each test.

Path analysis was used to evaluate how spatial heterogeneity, movement complexity, and information acquisition interact to influence foraging performance. Path analysis is a form of multiple regression that allows partitioning the correlation among the variables into direct and indirect causal relationships according to a priori hypothesis, the path diagram (Wooton 1994, Sokal & Rolf 1995). In a path diagram, the standardized partial regression coefficients (path coefficients) represent the direct effects of the independent variable (predictor) on the dependent variable (criterion), while all other independent variables remain constant. These path coefficients indicate the sign of the interaction and they represent the amount of change experienced by the dependent variable due to a unit change in the independent variable. The magnitudes of indirect effects are calculated as the sum of the products of the path coefficients that link a predictor with a criterion variable through other variables in the path diagram. Total effects are the sum of direct and indirect effects.

The strength of path analysis lies in its potential for evaluating specific structural models capable of statistical falsification (Sokal & Rolf 1995, Shipley 1997, Smith et al. 1997). However, this tool have to be used when the structure of the path diagram is based in a theory and solid natural history (Mitchell 1992). Previous studies on foraging behavior have successfully applied this statistical technique (e.g. Burrows & Hughes 1991, Morse & Stephens 1996, Kause et al. 1999, Johnson et al. 2001). I constructed the path diagrams of Fig. 6 (see legend for more details) based in background on the constrains that habitat heterogeneity imposes to locomotion and foraging in ants (e.g. Fewell 1988, Crist & MacMahon 1992, Crist & Haefner 1994, Crist & Wiens 1994), the increases in feeding performance due to information transfer in ants (e.g. Johnson 1991, Adler & Gordon 1992, Gordon et al. 1993, Roces & Nuñez 1993, Haefner & Crist 1994), and I assumed a direct effect of movement complexity on foraging efficiency (e.g. trajectories with a spatial pattern in straight line imply a greater resource removal rate). The sample size for this analysis should be at least 5-20 times larger than the number of estimated paths to ensure reliable results (Petraitis et al. 1996, Smith et al. 1997). My ratio sample size / paths number was of 6, and this value surpasses the lower range used in the majority of ecological studies (Smith et al. 1997).

I carried out the path analysis with EQS 5.7 software (Multivariate Software, Inc). This program is based on structural equation modeling that allows evaluating the statistical significance of the path diagram using maximum-likelihood technique. Model fit was evaluated using a χ^2 statistic, in which the covariance structure of the observed data is compared with the expected data if the model was true. A significant goodness of fit test indicates that the model is a poor description of the observed covariance among the variables, while a not significant value indicates that the pattern of covariance predicted by the model is not distinguishable from observed, and thus has a good fit to the data. A value of at least 0.95 in the Bentler-Bonett index was used as criterion of an acceptable approximate fit (Shipley 2000). The significance of path coefficients was evaluated with *t*-tests associated to multiple regression analysis (Mueller 1996).

RESULTS

Activity patterns and head contacts

The number of active workers removing prey from the food patch was significantly affected by exploitation time, but not by patch distance and the interaction between both factors (Table 1). When the food patch was located at a distance of 10 cm, the number of workers (10.60 ± 2.63, mean ± SE, n= 10 colonies) was a 26% greater than at distances of 20 cm (7.80 ± 1.03, n= 10 colonies), and 48% greater than at distances of 40 cm (5.50 ± 1.51, n= 10 colonies) (Fig. 1). The maximum number of foragers was reached at 0.8 of the total time of patch exploitation at distances of 10 cm, 0.6-0.7 of the total time at distances of 20 cm, and at 0.3 of the total time at distances of 40 cm (Fig. 1). There was a positive and significant relationship between the number of foragers and the number of head contacts per capita per trip at distances of 10 cm (r^2= 0.82, t= 5.99, $p < 0.001$), 20 cm (r^2= 0.70, t= 4.06, $p < 0.01$), and 40 cm (r^2= 0.69, t= 4.22, $p < 0.01$). Figure 2 shows this information for the three distances.

Route index

Route index (i.e. the ratio between path length / distance in straight line from patch to the nest) was significantly affected by exploitation phase, but not by patch distance and interaction between both factors (Table 2). During the initial exploitation phase the route index (1.75 ± 0.06, mean ± SE) was a 11% greater than during the half phase (1.56 ± 0.05), and 12% greater than during the final phase (1.54 ± 0.04) (Fig. 3, and see Fig. 4).

Removed preys, exploitation time, and capture rate

The number of captured prey by colony was significantly lower when the food patch was more distant from the nest entrance ($F_{2,30} = 7.82$, $p < 0.01$; see Fig. 5a). At distances of 10 cm the colonies captured 93.4 ± 4.2 microspheres of sugar (mean ± SE, n= 10 colonies, range: 57-100), 74.4 ± 9.9 microspheres (n= 10 colonies, range: 14-98) when the patch was 20 cm distant, and 42.4 ± 11.8 (n= 10 colonies, range: 1-100) when it was at 40 cm. The time invested in patch exploitation was significantly larger when the resource patch was more distant from the nest ($F_{2,30} = 25.02$, $p < 0.0001$; see Fig. 5b). At distances of 10 cm the colonies invested 32.6 ± 5.4 minutes (range: 15-61), 41.3 ± 5.5 minutes (range: 25-76) when the food was at 20 cm, and 118.2 ± 13.6 (range: 55-200) when it was at 40 cm. Resource removal rate was significantly lower when the food patch was more distant from the nest entrance ($F_{2,30} = 15.35$, $p < 0.0001$; see Fig. 5c). At distances of 10 cm the colonies removed 3.7 ± 0.6 food items per minute (range: 0.9-6.7), 2.2 ± 0.4 preys per minute (range: 0.2-3.9) at 20 cm, and 0.5 ± 0.2 (range: 0.01-1.8) at 40 cm.

Path analysis

The path diagram of Fig. 6a showed a poor description of the observed covariance among the variables ($\chi^2 = 17.455$, df = 2, $p < 0.001$). On the other hand, the model of Fig. 6b shows a good fit to the data ($\chi^2 = 2.099$, df = 1, p = 0.147), however, the value of Bentler-Bonett index (0.894) does not reach the criterion for an acceptable aproximate fit. Finally, correlations generated for the path diagram of Fig. 6c did not differ significantly from the observed correlations among variables ($\chi^2 = 0.235$, df = 1, p = 0.628). This model shows a good fit with the structure of covariance of the data (Bentler-Bonett normed fit index = 0.987), suggesting that the hypothetical causal relationships established between the predictor and the criterion variables are statistically valid. Figure 6c shows that the spatial heterogeneity and movement complexity have a negative but not significant direct effect on foraging performance (see Table 3). On the other hand, information use has a positive and significant direct effect on resource removal rate. The indirect effect of the spatial heterogeneity on foraging has a value of - 0.163 ([0.008 x - 0.062] + [- 0.269 x 0.605]), and its total effect - 0.351 ([- 0.188] + [- 0.163]). This path analysis model explains 47% of the total variance in foraging performance, 7% of the variance in information acquisition, and less than 1% of the variance in movement complexity (see Table 4). This analysis was carried out for different time phases (initial, half, and final), and I found similar results. However, the model explains a greater percentage of the total variance in foraging performance through exploitation time (23%, 51%, and 62%, for initial, half, and final exploitation phase, respectively).

DISCUSSION

The reduced number of active foragers when the food patch was located at a greater distance from the nest entrance can be due to constrains present in the matrix. An important factor that affect the foraging behavior of ants is mortality risk (e.g. Nonacs

1990). At greater path lengths and longer time invested in foraging trips, there is an increase in loss of thermal balance (e.g. Lighton & Bartholomew 1988) and/or predation-parasitism risks (e.g. Feener & Moss 1990). The habitat associated to distant resource patches represents a more dangerous area that trigger lower recruitment (e.g. Nonacs & Dill 1988, 1990). On the other hand, a lower number of active ants is related with fewer head contacts between workers during their inbound travel, restricting information transfer about location and quality of a novel food patch and possibly determining a lower recruitment (e.g. Gordon 1999). The spatial heterogeneity correlated with large distances can dilute the recruitment earlier due to physical barriers that obstructs the movements and/or communication between foragers. This would explain the pattern of foraging at distances of 40 cm, where the maximum number of workers is reached quickly, but afterwards the activity level diminishes.

Compared with other insects and vertebrates, ants exhibit a high movement complexity (e.g. Fourcassié et al. 1992, Wiens et al. 1995). However, the complexity of a movement path is not static, but dynamic, where the spatial pattern of the tracks can depend on the stimulus that triggers their expression and on information acquisition from the environment throughout time. In this study, I focused my attention on foraging movements, and I found that during patch exploitation the complexity of trajectories decreased. This can be interpreted as a strategy of spatial navigation, which basically consist in the generation of movements reaching short straight lines that allow the avoidance of obstacles in the space (e.g. Collet 1996, Wehner et al. 1996). Despite the scarcity of knowledge about mechanisms of communication in the genus *Dorymyrmex*, I propose that possibly *D. goetschi* foragers use their visual system to recognize familiar landmarks in the landscape and/or use trail pheromones secretions for marking ways in the substratum. Both mechanisms would increase locomotion performance.

When food patches were at greater distance from the nest entrance, fewer prey were captured, more time was invested in patch exploitation, and therefore, colonies obtained lower resource removal rates. These results are also related to a low number of active foragers at larger distances. A lower rate of recruitment with increasing patch distance has been documented for species of ants moving at different spatial scales (e.g.

Hölldobler 1976, Taylor 1977, Fewell et al. 1992). In food patches located at larger distances, a mechanism of positive feedback is activated between the amount of active workers, successful returns, and ants that leave the nest to foraging. That is, if a threshold value in the number of captured prey by time unit is not exceeded at the beginning of the patch exploitation, a low recruitment of individuals will take place. This would reflect the sensitivity whereupon colonies fit their activity of foraging according to the availability of resources and environmental conditions (e.g. Gordon 2002).

Contrary to expectations, landscape spatial heterogeneity did not have a significant effect on foraging performance. This finding can be explained by the perception that ants have, which allows them to recognize habitat structure with coarse-grain (*sensu* Levins 1968). These insects do not walk over but through a landscape (Kaspari & Weiser 1999), and with their small body size and short legs length they can perceive a high number of environmental interstices (i.e. environmental rugosity) (Farji-Brener et al. 2004), and thus exploit environments where the resources are patchily distributed (e.g. Kaspari 1993, Wiens et al. 1995).

Movement complexity does not have a significant effect on foraging performance, possibly the value of the route index for total removal rate can disguise the real influence of path length on feeding performance. The analysis of changes in the route index during different phases of the patch exploitation supports this assumption, since only in the initial phase, trajectories were more complex and only afterwards these had a less sinuous pattern (see Fig. 3). On the other hand, the tendency of a negative effect of the spatial heterogeneity and movement complexity on the foraging efficiency is coincident with my first and second predictions mentioned in the introduction. A greater sample size could help to determine if these factors have a significant biological influence.

Ants of the species *D. goetschi* exhibit mainly individual foraging but sometimes they can present a diffuse recruitment (Oster & Wilson 1978, Hölldobler & Wilson 1990). This study shows that while a large number of active workers moved between the patch and the nest, a greater number of antennal contacts per capita among the foragers takes place, resulting in a greater resource removal (see Fig. 6c). Increases in the performance of foraging tasks due to collective work by ants has been well documented in the literature (see Detrain et al. 1999 for a revision). The tasks of individual ants are integrated in a organized work at the level of the colony, due to that the collective exploration of scouts workers allowing quickly discovery of a food patch and effective recruitment (e.g. Beckers et al. 1989, Devigne & Detrain 2002). Besides, in some occasions the colonies of *D. goetschi* partitioned foraging tasks, displaying a process of relay with indirect transfer of prey, in dump site, during patch exploitation (H. Torres-Contreras, personal observation). This last behavior reduces individual foraging time and introduces redundancy to the feeding activities, therefore increasing reliability in the performance of foraging tasks (e.g. Anderson & Ratnieks 1999, Ratnieks & Anderson 1999).

The foraging behavior in ants is determined by multiple variables. In a spatial scale equal or lower to 40 cm, however, substrate heterogeneity does not have significant effects (direct and indirect) on the foraging success of *D. goetschi* colonies. Similarly, the path length of workers do not have influence on resource removal rate. Only the information transfer between nestmates has a direct effect on feeding performance. Therefore, the results of this study shows that this ant species have a high resolution of perception, defines quickly the individual foraging routes, and the number of workers and antennal contacts account for a large fraction of the intrinsic variation of their feeding behavior.

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LEGEND OF FIGURES

Figure 1: The effect of exploitation time and resource patch distance on the number of *D. goetschi* active workers foraging between the nest and food patch. The exploitation time is expressed in relative terms for comparison. Values are mean ± SE. See Table 1 for details.

Figure 2: The relationship between the number of foragers and the number of head contacts per capita per inbound trip in *D. goetschi* colonies. The sample size was n= 10 colonies for each distance treatment. Values are mean. See text for details.

Figure 3: The effect of exploitation phase and food patch distance on the ratio between path length and distance in straight line from patch to the nest (route index) of *D. goetschi* foragers. Values are mean ± SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See Table 2 for details.

Figure 4: Representative trajectories of *D. goetschi* individuals from a food patch (open circle) located at 10 cm from the entrance of the nest (black circle) during the **(a)** initial and **(b)** final phase of resource exploitation.

Figure 5: The effect of food patch distance on **(a)** the number of captured prey, **(b)** duration of patch exploitation, and **(c)** resource removal rate carried out by *D. goetschi* colonies. Values are mean ± SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See text for details.

Figure 6: Path diagrams (**a**, **b**, **c**) for the effects of spatial heterogeneity, movement complexity, and information acquisition on the foraging success of *D. goetschi* colonies. The sample size was n = 30 colonies. Unidirectional arrows indicate direct relations (solid lines represent positive paths, and dashed lines represent negative paths). The terminology * and NS located next to the arrows indicate significant and not significant statistically path coefficients, respectively. The residual variable (U) represents the unmeasured factors that affect each dependent variable; and the path coefficient for U was calculated as $(1 - R^2)^{1/2}$ for the R^2 of the multiple regressions. * $P < 0.001$.

Figure 1

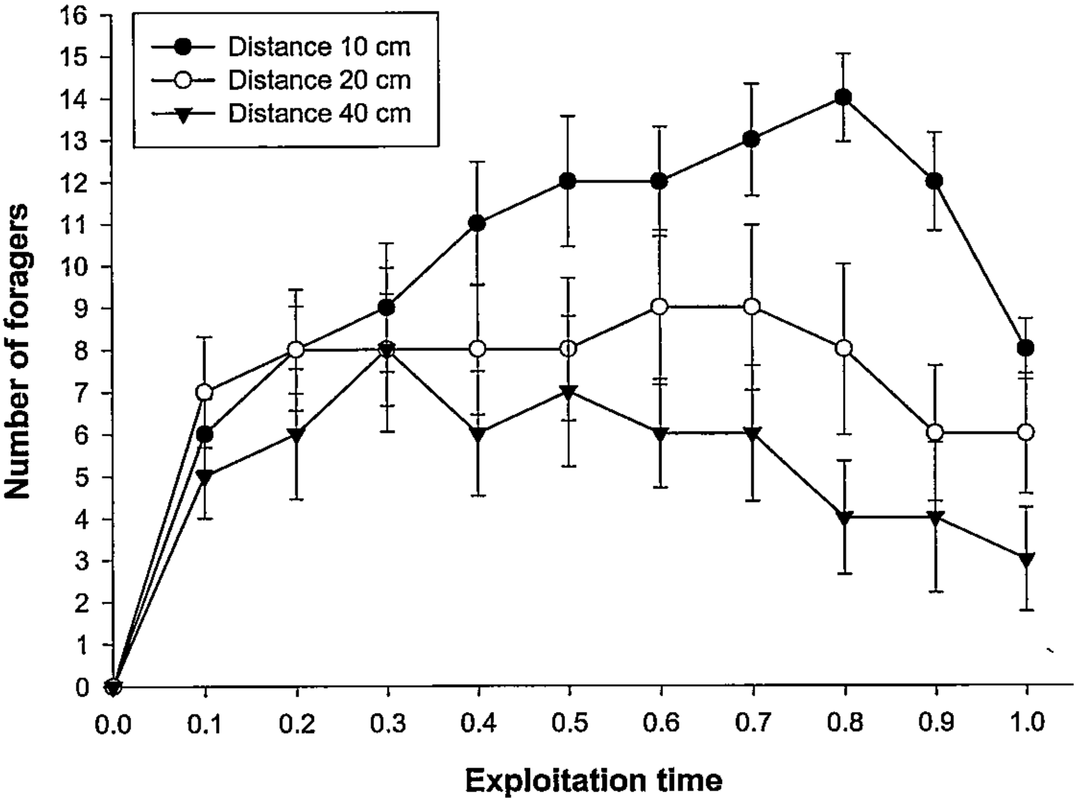

Distance 10 cm
Distance 20 cm
Distance 40 cm
Number of foragers
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Exploitation time

Figure 2

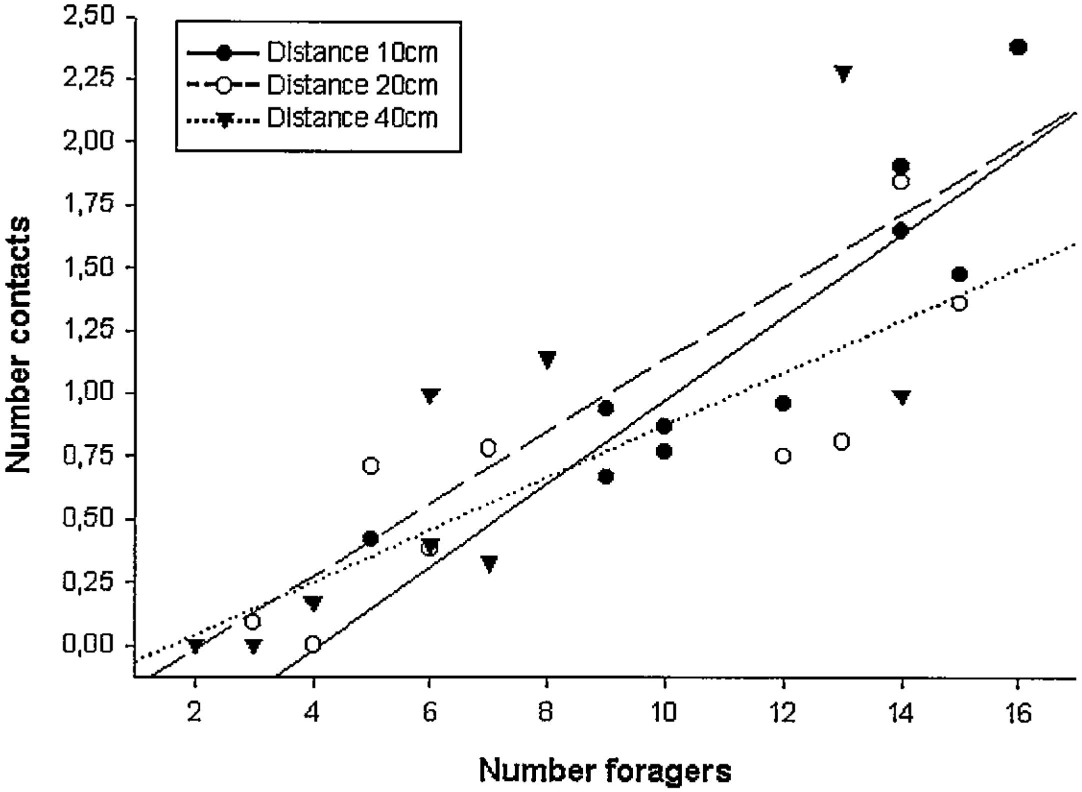

2,50
2,25
2,00
1,75
1,50
1,25
1,00
0,75
0,50
0,25
0,00
Number contacts
Distance 10cm
Distance 20cm
Distance 40cm
2
4
6
8
10
12
14
16
Number foragers

Figure 3

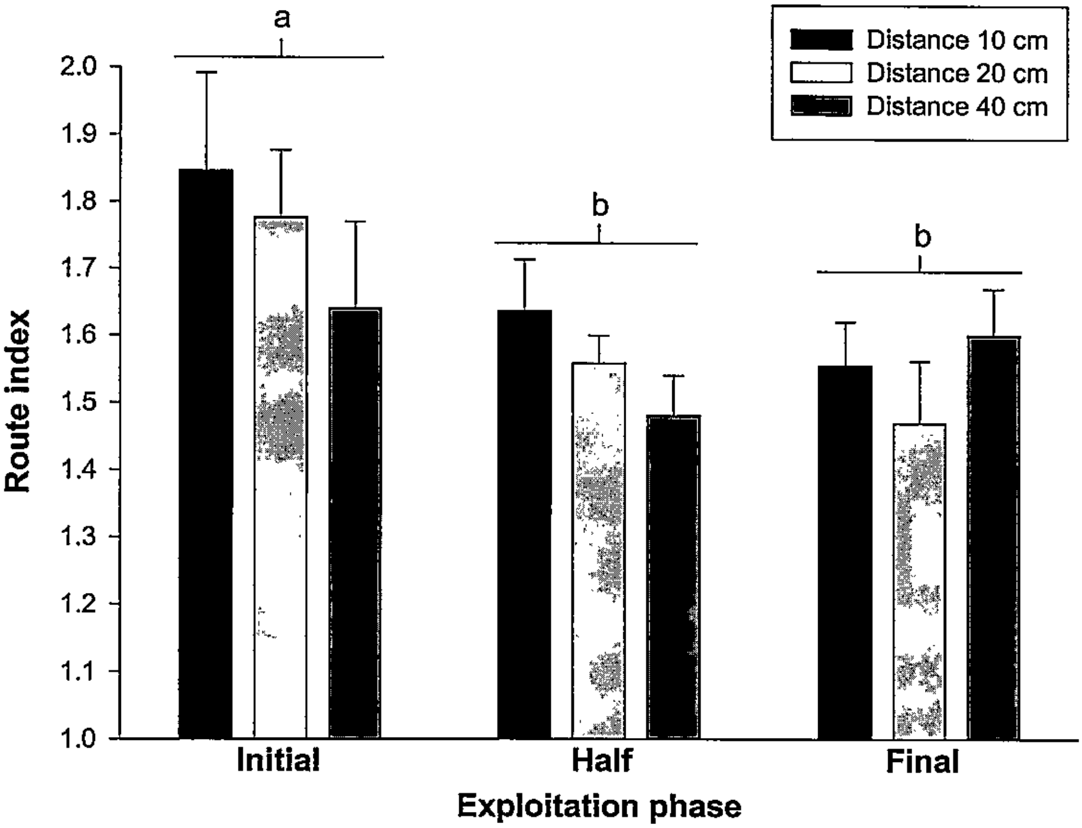

a
b
b
Distance 10 cm
Distance 20 cm
Distance 40 cm
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
Route index
Initial
Half
Final
Exploitation phase

Figure 4

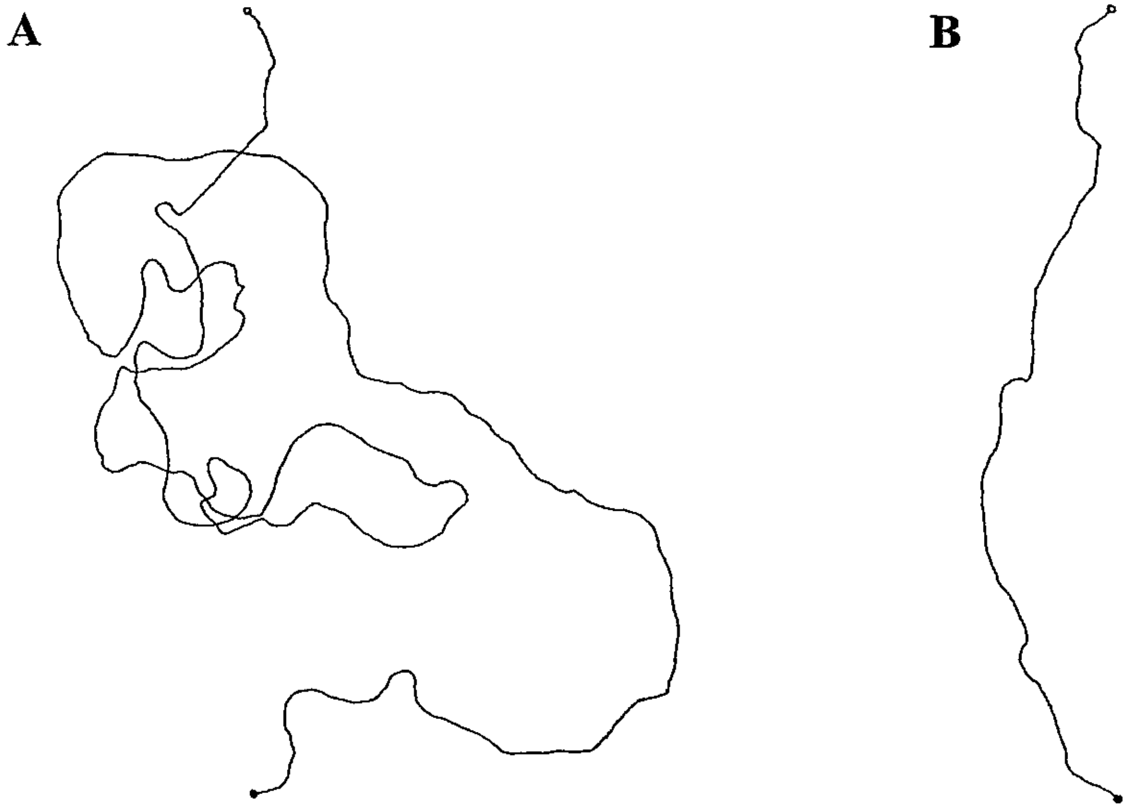


Figure 5

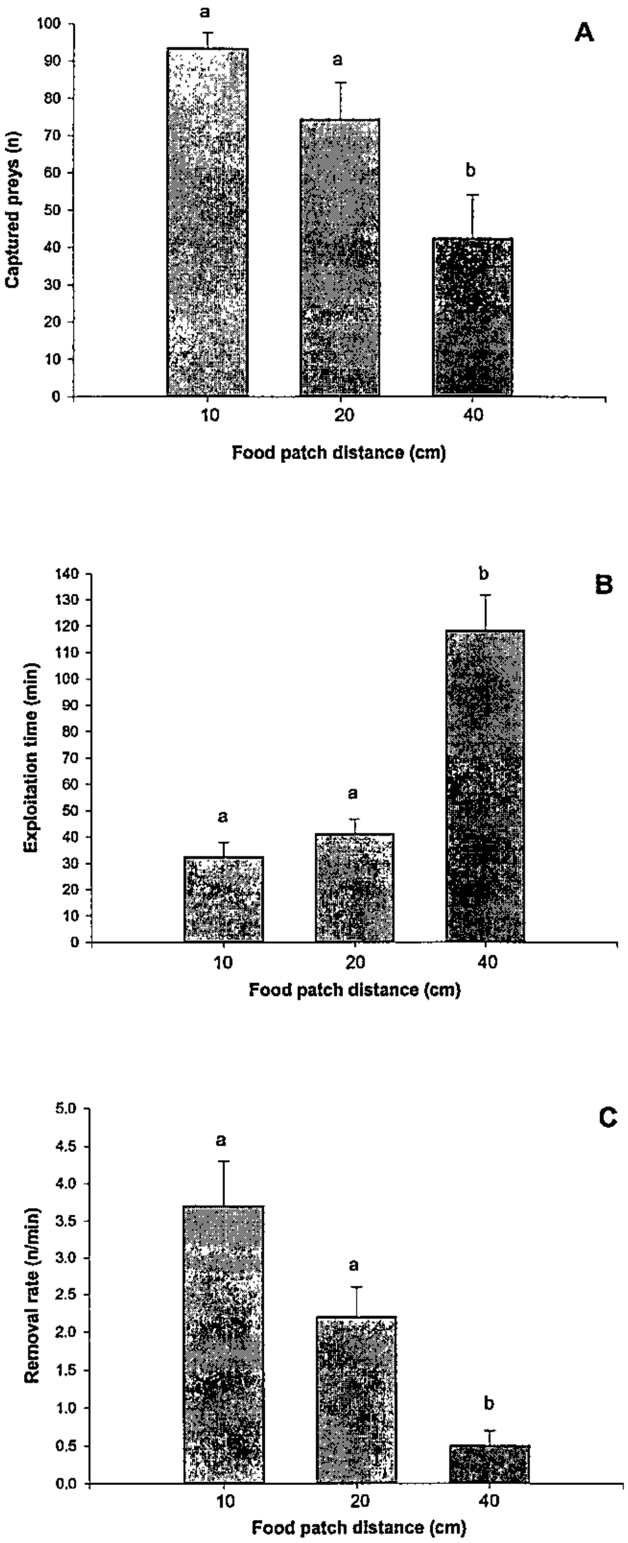

A
Captured preys (n)
100
90
80
70
60
50
40
30
20
10
0
a
a
b
10
20
40
Food patch distance (cm)
B
Exploitation time (min)
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
a
a
b
10
20
40
Food patch distance (cm)
C
Removal rate (n/min)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
a
a
b
10
20
40
Food patch distance (cm)

Figure 6

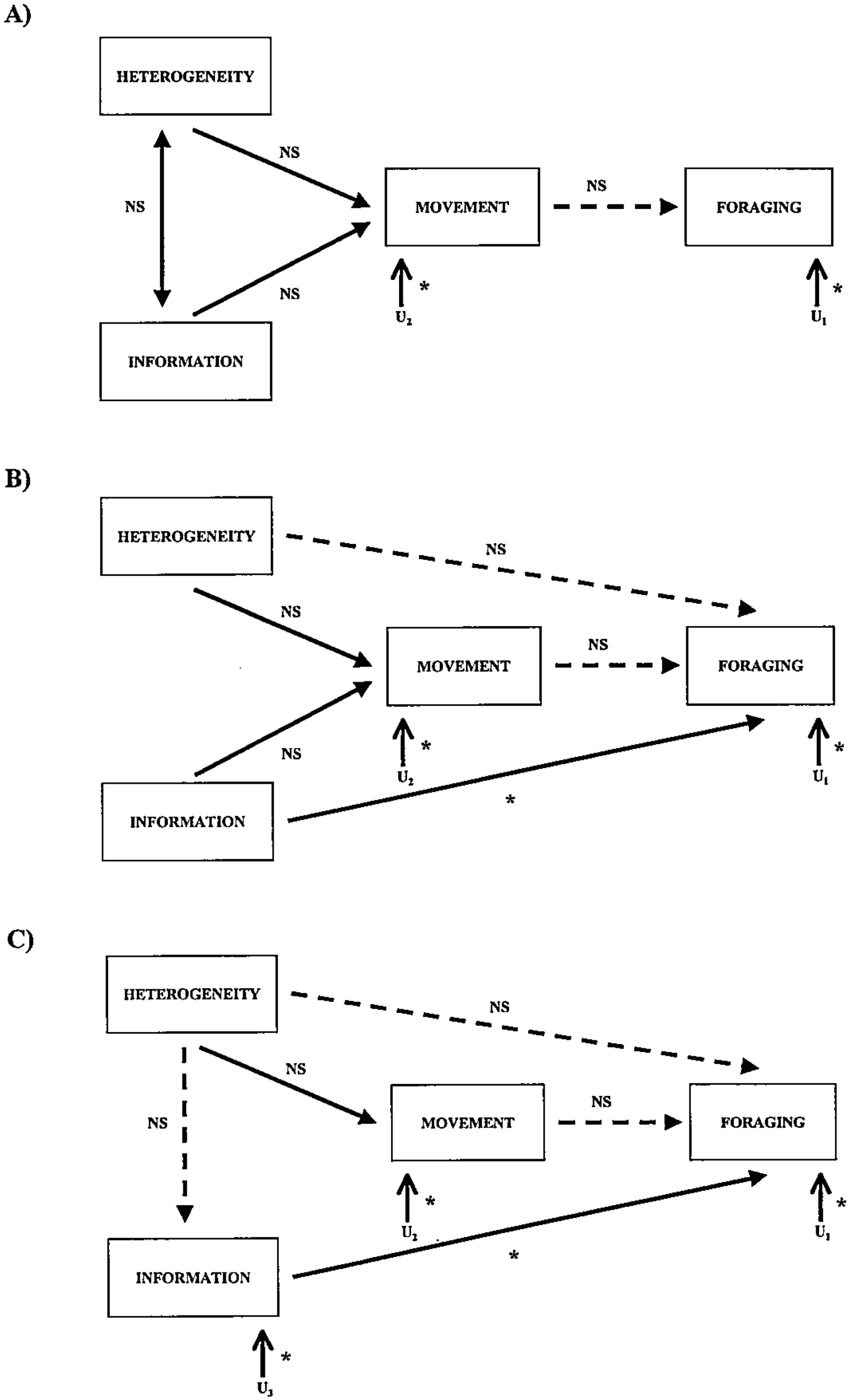

A)
HETEROGENEITY
NS
NS
NS
MOVEMENT
NS
FORAGING
INFORMATION
*
U_2
*
U_1
B)
HETEROGENEITY
NS
NS
MOVEMENT
NS
FORAGING
NS
*
U_2
*
U_1
INFORMATION
*
C)
HETEROGENEITY
NS
NS
NS
MOVEMENT
NS
FORAGING
*
U_2
*
U_1
INFORMATION
*
*
U_3

Table 1. Results of a two-way ANOVA for the effects of exploitation time and resource patch distance and their interaction on the number of *Dorymyrmex goetschi* foragers. The colony (C) was utilized as covariate.

Source	df	SS	MS	F	P
Time	9	390.672	43.408	2.109	0.029
Distance	2	16.004	8.002	0.389	0.678
Time x Distance	18	402.930	22.385	1.087	0.365
Covariate (C)	1	79.900	79.900	3.881	0.049
Error	259	5332.033	20.587		

Table 2. Results of a two-way ANOVA for the effects of exploitation phase and food patch distance and their interaction on the route index of *Dorymyrmex goetschi* foragers. The colony (C) was utilized as covariate.

Source	df	SS	MS	F	P
Phase	2	0.744	0.372	4.619	0.013
Distance	2	0.162	0.081	1.010	0.369
Phase x Distance	4	0.216	0.054	0.673	0.613
Covariate (C)	1	0.076	0.076	0.949	0.333
Error	71	5.680	0.080		

Table 3. Measurement equations and test statistics by each multiple regression model used to build the path diagram. The H_0 corresponds to the null hypothesis, i.e. parameter = 0.

Dependent variable	Independent variable	Parameter estimate	Standard error	*t* for H_0	P
Foraging	Spatial heterogeneity	-1.155	0.878	-1.316	0.198
	Movement complexity	-0.741	1.639	-0.452	0.655
	Information acquisition	0.273	0.065	4.228	<0.001
Movement	Spatial heterogeneity	0.004	0.097	0.045	0.964
Information	Spatial heterogeneity	-3.649	2.472	-1.476	0.151

Table 4. Standardized path coefficients and the proportion of variance explained (R^2) by each multiple regression model used to build the path diagram. The U is unexplained variation for each dependent variable. * $P < 0.001$.

Dependent variable	Independent variables	Path coefficient	R^2	U
Foraging efficiency	Spatial heterogeneity	-0.19	0.47	0.73*
	Movement complexity	-0.06		
	Information acquisition	0.61*		
Movement complexity	Spatial heterogeneity	0.01	<<0.01	1.00*
Information acquisition	Spatial heterogeneity	-0.27	0.07	0.96*

CAPÍTULO 2

A field experiment on the influence of load transportation and patch distance on the locomotion velocity of *Dorymyrmex goetschi* (Hymenoptera, Formicidae)

SUMMARY

Locomotion velocity during foraging activities is determined by factors such as travel distance, habitat structure and load mass among others. However, few studies on foraging behavior have analyzed the influence of spatial heterogeneity and food transportation on the locomotion velocity of ants under natural conditions. In order to study the mentioned factors, I selected 20 nests of the ant *Dorymyrmex goetschi* (subfamily Dolichoderinae), in a lower Andes locality of central Chile. Half of the nests were offered a food patch located at 10 cm from the nest entrance, and at 20 cm for the other half. I measured the duration of trips between nest and food patch and vice versa, and the distances traveled. I also recorded spatial heterogeneity of the substratum and soil temperature. Temperature was used as a covariate in the statistical analysis. Travel speed was significantly slower when worker ants returned to the nest with a food load, compared to the velocity of foragers without load that traveled from the nest to the patch. When the food patch was located at greater distance, locomotion velocity was significantly faster. Spatial heterogeneity did not affect movement speed. The reduction in locomotion velocity in ants carrying a load of 5.6 mg represents an energetic cost of transportation equivalent to 79% of the costs involved in moving a body mass of 1.6 mg. Faster velocities at larger patch distances can be interpreted as a strategy to maintain an efficient resource exploitation, by way of decreasing the time exposed to higher predation risk.

Key words: Ants, load burden, food patch, spatial heterogeneity

INTRODUCTION

Locomotion velocity is an animal characteristic that determines the performance of other behaviors such as escape from predators, food searching, and exploration of the environment. In terrestrial artrophods like crabs (e.g., Herreid and Full, 1986b), cockroaches (e.g., Herreid et al., 1981), beetles (e.g., Bartolomew et al., 1985) and ants (e.g., Nielsen et al., 1982), the analysis of this attribute has been centered in the energetic costs and biomechanical aspects associated to pedestrian locomotion. Locomotion velocity can be influenced by habitat structure and food transportation. For example, in hermit crabs, velocity is a function of prey size and substratum, where crabs with lighter load move faster and more efficiently in sand that in rocky substratum (Herreid and Full, 1986a,b).

During the exploration of new areas, ants normally move in a complex form and at low speed, presenting trajectories with high superimposition and larger covered area (Deneubourg et al., 1983; Hölldobler and Wilson, 1990). However, after finding and capturing prey, ants return to the nest with a more linear trajectory and at a greater speed (Johnson, 1991; Herbers and Choiniere, 1996). This behavior would be the result of learning about the location and richness of food patches through the use of familiar marks in the landscape, which would allow workers to reduce their travel and food searching times (Johnson, 1991; Collet, 1996). However, other factors such as nutritional quality of food (e.g., Roces, 1993), environment temperature (e.g., Marsh, 1985), encounter rates between workers (e.g., Burd and Aranwela 2003), body size (e.g., Burd, 2000), vegetation cover (e.g., Fewell, 1988) and load (e.g., Lighton et al., 1993), can influence locomotion velocity of ants. In particular, areas with high vegetation cover can diminish running speed of harvester ants (Fewell 1988). On the other hand, although forager ants can carry preys as large as 10-20 times their body weight, transportation of large loads reduces locomotion velocity (Nielsen et al., 1982; Lighton et al., 1987).

There are few studies on foraging behavior under natural conditions that analyze the influence of habitat structure and food transportation on the locomotion velocity of ants. Field experiments would allow answer the questions: can food patches located at different distances from the entrance of the nest produce changes in locomotion velocity? Is locomotion velocity affected by the load transportation and landscape heterogeneity at low range spatial scale? In this context, the aim of this study was to analyze the effect of resource patch distance, food transportation, and spatial heterogeneity, on the locomotion velocity in a common central Chilean ant. Results are discussed in terms of energetic and time costs that individuals incur during foraging.

METHODS

Study site and species

The fieldwork was conducted in the Rio Clarillo National Reserve (33° 51' S, 70° 29' W), a lower Andes locality of central Chile situated 45 km SE of Santiago. Vegetation is composed mainly by evergreen sclerophyllous woody plants, and annual and perennial herbs (Gajardo, 1993). The climate is a cold temperate regime with precipitation concentrated during the winter and a dry period of about seven months around summer.

The studied species was *Dorymyrmex goetschi* Menozzi 1935, which belong to the subfamily Dolichoderinae (Snelling and Hunt, 1975; Shattuck, 1992). The workers of this species have red coloration in head and thorax, a black abdomen, and a body mass of 1.63 ± 0.01 mg (mean ± SE, n= 506). These ants construct their nests in open spaces without tree or shrub vegetation. The entrance of the nest has a characteristic earth hillocks produced by rubble removed from the interior by the ants. The daily activity of ants begins at dawn with a period of nest cleaning, proceeding afterwards with a period of exploratory and foraging activities. These activities are performed until soil temperature reaches 45° C. At this temperature the entrance of the nest is closed with vegetable material and activities cease above ground (Torres-Contreras, pers. obs.). This species has been documented as belonging to the assembly of harvester ants (Medel and Vásquez, 1994; Torres-Contreras, 2001). Analysis of natural prey transported to the nest shows that this species incorporates insects to its diet in a percentage of 27-47% (Torres-Contreras, unpubl. data). *Dorymyrmex goetschi* constitutes together with *Camponotus chilensis* and *C. morosus*, one of the most common ant species present in the study site (Torres-Contreras, pers. obs.).

Experimental design

The fieldwork was carried out between late October and early December 2001 during the spring season. In the field, *D. goetschi* transport natural loads with a mass of 0.97 ± 0.07 mg (mean ± SE, n= 506, range 0.002 - 13.542 mg). I used as prey, compacted sugar microspheres (5.6 mg ± 0.05, mean ± SE, n= 100). Although the size of the experimental food items was in the upper range of the natural prey distribution, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey variability was low or nil. Further, our observations revealed that prey handling was not affected by these prey items. I selected 20 nests of *D. goetschi* to which we offered a food patch of 100 microspheres. To 10 colonies selected at random we placed the food patch at a distance of 10 cm from the nest entrance, and to the other 10 colonies the resource patch was located at a distance of 20 cm. These distances were within the normal foraging range of this species (i.e., 0.0-2.0 m; Torres-Contreras, pers. obs.). Resource patches were set at 8:00 AM and I video recorded (Sony camera, model CCD-TR818) the movement and feeding behavior of forager workers until the resource was depleted and/or the activity stopped. Video records were watched to measure the duration of trips from the nest to the food patch and vice versa. Subjects moving from the nest to the patch carried no load and were exploring the environment, and subjects moving from the patch to the nest transported one food load per trip (one microsphere in all cases). I could not gather data on ant movement with no-food from the patch to the nest for all colonies, because few subjects returned to nest with no food, and when this happened, subjects moved more erratically (possibly extending their exploratory range), and hence they went outside the video recording area. However, I obtained data on a few colonies showing that ants carrying no food item moving in either direction showed similar speeds (t= 0.76, p = 0.49, n= 6). Therefore, any effect of prey transportation on velocity could be attributable to load. The trajectories of individuals between both points in the space were traced in transparent films put directly over a video monitor. These trajectories were measured by using SigmaScan software (SPSS Inc.). With the measurements of distance and time I estimated average locomotion velocities.

In the field, I measured environmental temperature around each colony at two millimeters above the soil with a digital thermometer (Checktemp, precision ± 0.1° C). Landscape spatial heterogeneity was estimated with linear transects that were arranged through the matrix that separated the entrance of the nest and the food patch. Following Johnson et al. (1992), I calculated a heterogeneity index that considers the proportion of ground surface covered by some physical element that could inhibit ant locomotion (e.g., stones, twigs, leaves, and/or grass; 2 mm wide and long or larger), in relation to the total surface that include bare ground. For example, if 1 cm is covered by twigs, out of a total distance of 10 cm, then the heterogeneity index has a value of 0.1.

The influence of patch distance, load transportation, and the interaction between both factors on the locomotion speed was analyzed with a two-way ANOVA, with soil temperature used as covariate, and colony as the sample unit. Hence data correspond to the mean of foragers per colony (the range of the number of workers for 10 cm distance was 10-60 for outbound travels and 24-82 for inbound travels; and for 20 cm distance was 7-56 and 11-74, respectively). Simple linear regressions were used to analyze the relationships of soil temperature and landscape heterogeneity with locomotion speed. All tests were carried out with Statistica 6.0 software (StatSoft Inc.). Data shown correspond to the mean ± one standard error, and the significance of the statistical tests was fixed to $\alpha = 0.05$. Data satisfied the assumptions of each test.

RESULTS

Effect of patch distance and food load

The locomotion velocity of workers without load that travel from the nest to the food patch (outbound direction) and of foragers that transported a food load from the food patch to nest (inbound direction) were: 1.90 ± 0.12 cm/s (mean ± SE) for outbound to 10 cm distances (n= 10 colonies), 1.58 ± 0.13 cm/s for inbound from 10 cm (n= 10 colonies), 2.63 ± 0.16 cm/s for outbound to 20 cm (n= 10 colonies), and 1.91 ± 0.14 cm/s for inbound from 20 cm (n= 10 colonies). The locomotion speed of foragers was significantly affected by patch distance and food transportation, but not by the interaction between both factors (Table 1). Locomotion speed was faster at 20 cm than at 10 cm for both outbound and inbound trips (Fig. 1).

Effect of soil temperature and spatial heterogeneity

There was a positive and significant relationship between soil temperature and locomotion velocity for outbound workers (r^2= 0.32, t = 2.86, $p < 0.05$; Fig. 2a). The equation that relates both variables is: $V = 0.56 + 0.06 (T)$, where V corresponds to speed and T is temperature. Similarly, there was a positive and significant relationship between soil temperature and locomotion velocity for inbound foragers (r^2= 0.46, t = 3.84, $p < 0.01$; Fig. 2b). The equation that relate both variables is: $V = 0.03 + 0.07 (T)$. On the other hand, there was not significant relationship between landscape spatial heterogeneity and locomotion velocity. Nevertheless, locomotion speed for outbound workers tended to be slower at greater spatial heterogeneity (r^2= 0.19, t = 2.02, p = 0.059; Fig. 3a). Locomotion speed for inbound foragers was not affected by spatial heterogeneity (r^2= 0.10, t = 1.38, p = 0.186; Fig. 3b).

DISCUSSION

Foragers of *D. goetschi* were able to transport food loads equivalent to 3.5 times their body mass. One of the immediate effects of food load transportation in ants is the reduction of locomotion velocity (see Fig. 1), which has been attributed to the energetic costs of transportation (Nielsen et al., 1982; Lighton et al., 1987, 1993). In fact, calculations of the minimum cost of transport in ant genera like *Messor* and *Pogonomyrmex* show that the transportation of a load unit involves an increase of 60% of the energetic costs of locomotion of a unit of body mass (e.g. Nielsen and Baron-Urbani, 1990; Lighton et al., 1993). Specifically, using equation 5 of Lighton et al. (1993), shows that in *D. goetschi* a load of 5.6 mg, represents a transportation cost of 79% of the cost involved in moving a body size of 1.6 mg. Transportation of loads also produces changes in the spatial pattern of leg coordination in ants, via a reduction of stride length necessary to compensate the forward shift of the center of body mass (Zollikofer, 1994). Therefore, load transportation modifies the relative burden over the legs and constrains locomotion velocity (Zollikofer, 1994).

The load burden ($B= M_b + M_l / M_b$, where M_b is body weight and M_l the load mass transported; see Rissing 1982) of the artificial prey transported in our experiments by *D. goetschi* has a value of B=4.5. This B reduced 25% the locomotion speed of *D. goetschi* foragers. A significant effect of load on locomotion has been reported in different ant species (Nielsen et al., 1982; Lighton et al., 1987, 1993; Burd, 2000). However, for B values between 1.1 and 1.5, locomotion speed is independent of load (Rissing, 1982). I found that natural prey had a B=1.6, which is within the range of B values reported in other studies for harvester ants of the genus *Pogonomyrmex* (Lighton et al., 1993; Weier et al., 1995). Interestingly, this B value implies that *D. goetschi* foragers transport a majority of natural loads that do not seem to modify their speeds, and in this way ants would increase their exploitation rate of resources.

The theory of central place foraging (Orians and Pearson, 1979; Schoener, 1979) predicts that with increasing distance of the resource patch to the nest, an organism will have to select prey of greater size and/or richer energy content to compensate the energetic costs and time investment involved in traveling greater distances. These models assume that load size does not affect travel time, and hence travel speed (see Wetterer 1989). Selection of larger and/or more energetic preys has been founded in harvester species of the genera *Pogonomyrmex* (Bailey and Polis, 1987; Crist and MacMahon, 1992; Morehead and Feener, 1998) and *Veromessor* (Rissing and Pollock, 1984), but not in *Messor* (see Baroni-Urbani and Nielsen, 1990). Nevertheless, several authors have suggested that for ants it is not so important to maximize the energetic returns but to minimize time investment, and thus to maximize the net acquisition of resources in a certain period of time (Fewell, 1988; Weier and Feener, 1995). In this study, prey size was the same for both distances, thus the increase in locomotion speed at longer distance cannot be attributable to load carriage only (see Wetterer 1989), and can be interpreted as a strategy that tend to maintain an efficient resource removal rate, particularly if other costs increase with distance and/or time exposed outside the nest. For example, decreasing the time involved in trips to and from the nest for longer distances may allow ants to maintain a certain level of predation risk, when this risk increases with distance from the nest (Feener and Moss, 1990). In fact, it has been observed that animals move faster under higher predation risk (Vásquez et al., 2002). In our study, ants might have experienced higher predation risk at longer distances from the nest, and therefore they might benefit by traveling faster to and from more distant patches. On the other hand, a higher encounter rate of foragers could also diminish locomotion speed due to interference during movement (Burd and Aranwela, 2003). If encounter rate is higher closer to the nest, as it would be expected, then speeds would be slower at shorter distances from the nest, as it was our case.

Our results show that *D. goetschi* is not a termophilic species, because the temperatures where the workers displayed activities were in the range of 14-42° C. Despite that during the course of experimental trials temperature increased steadily and hence contributed to increasing locomotion speed, higher velocities might also be the result of information processing at individual and colonial level (e.g. Johnson, 1991; Wehner et al., 1996). In laboratory experiments at constant environmental temperature, the movement speed of *D. goetschi* foragers is greater during the final phase of resource exploitation, probably due to the use of familiar landmarks in the landscape and/or chemical signals (Torres-Contreras and Vásquez, unpubl. data).

Several studies have found that increases in the complexity of movement are determined by the physical barriers that the landscape impose to the trajectories of organisms (e.g. With, 1994; Wiens et al., 1995). I have found that increases in habitat spatial heterogeneity produces movement paths with a more complex shape, that is, trajectories with high superimposition and greater fractal dimension (Torres-Contreras and Vásquez, unpubl. data). In this study, spatial heterogeneity did not affect locomotion velocity, which could be the result of changes in time expenditure during locomotion. Possibly, ants compensate an increase in trajectory sinuosity with faster movement. Therefore, it seems that when the temporal dimension is added to the spatial analysis of movement, the effect of landscape heterogeneity is not conclusive. The influence of habitat heterogeneity on the locomotion velocity can affect other behaviors. For example, fieldwork and laboratory experiments with *D. goetschi* have shown lower resource removal rates when confronted with a greater proportion of physical barriers in the landscape (Torres-Contreras and Vásquez, unpubl. data). Future studies should consider the stimuli that trigger movement decisions (e.g., food), the temporal dynamics of movement (e.g. information acquisition) and the implications on other behaviors (e.g. foraging efficiency), for a proper understanding of the influence of habitat structure on the locomotion of animals.

LEGEND OF FIGURES

Figure 1. The effect of resource patch distance and food transportation on the locomotion speed of *D. goetschi* foragers. The black bars represent speeds from the nest to the resource patch (outbound direction) and the white bars speeds in the reverse direction (inbound direction). Values are mean ± SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$).

Figure 2. The relationship between soil temperature and mean velocity of *D. goetschi* in outbound (**a**) and inbound (**b**) travels. In both cases $n = 20$ colonies. See text for details.

Figure 3. The relationship between landscape spatial heterogeneity and mean velocity of *D. goetschi* in outbound (**a**) and inbound (**b**) travels. In both cases $n = 20$ colonies. See text for details.

Figure 1

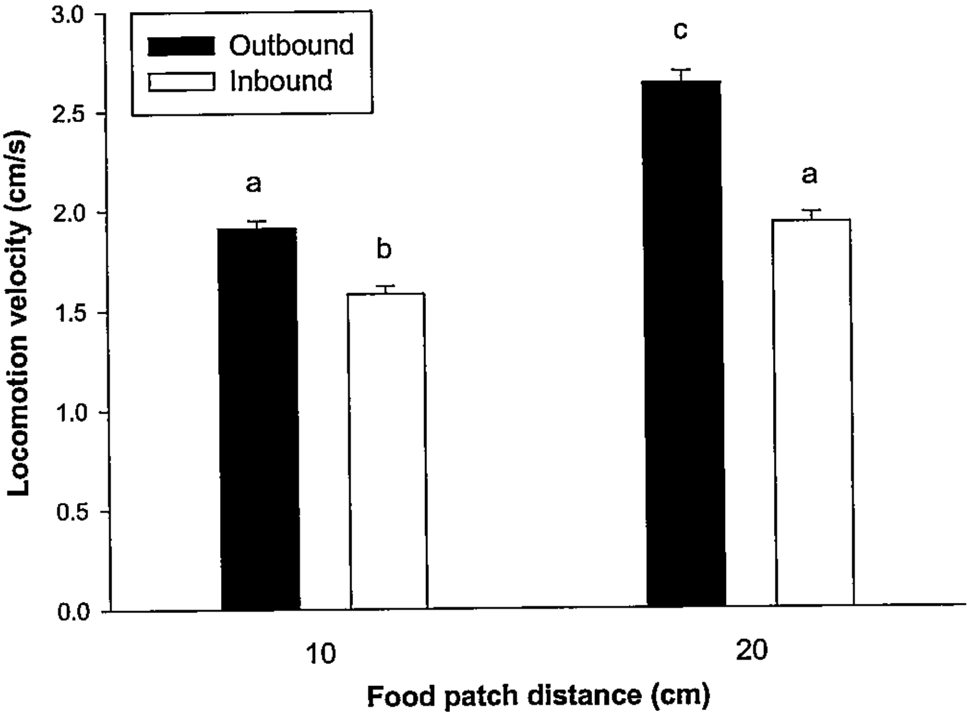
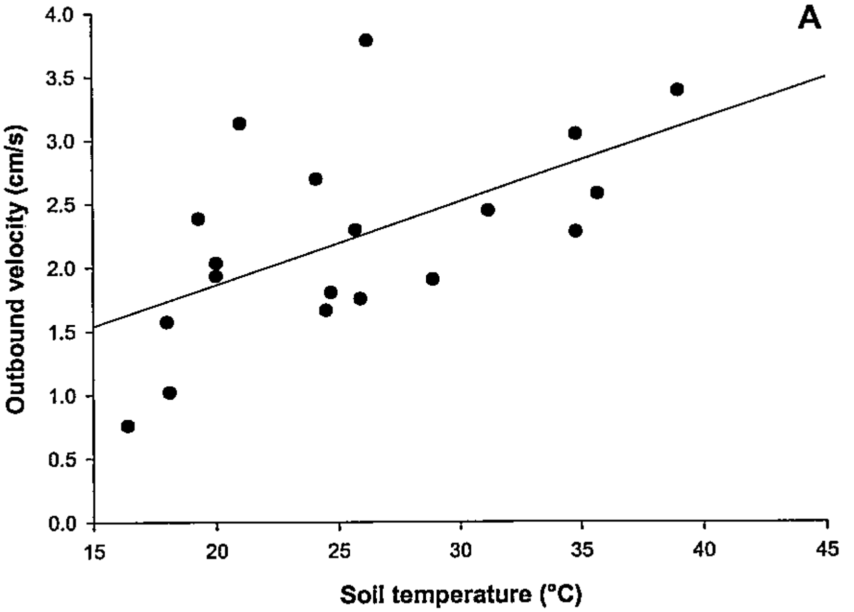

3.0
2.5
2.0
1.5
1.0
0.5
0.0
Outbound
Inbound
Locomotion velocity (cm/s)
a
b
c
a
10
20
Food patch distance (cm)

Figure 2


A
Outbound velocity (cm/s)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
15
20
25
30
35
40
45
Soil temperature (°C)

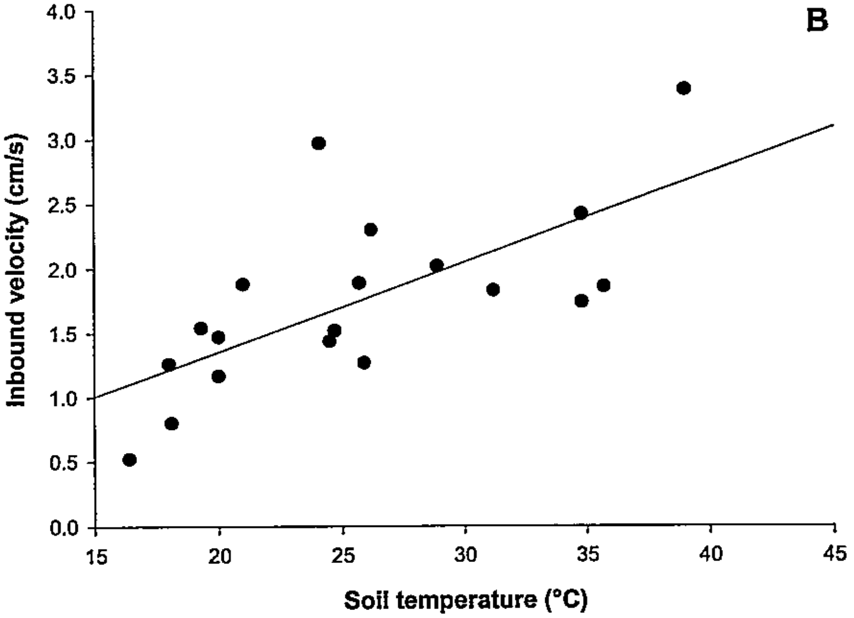

B
Inbound velocity (cm/s)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
15
20
25
30
35
40
45
Soil temperature (°C)

Figure 3

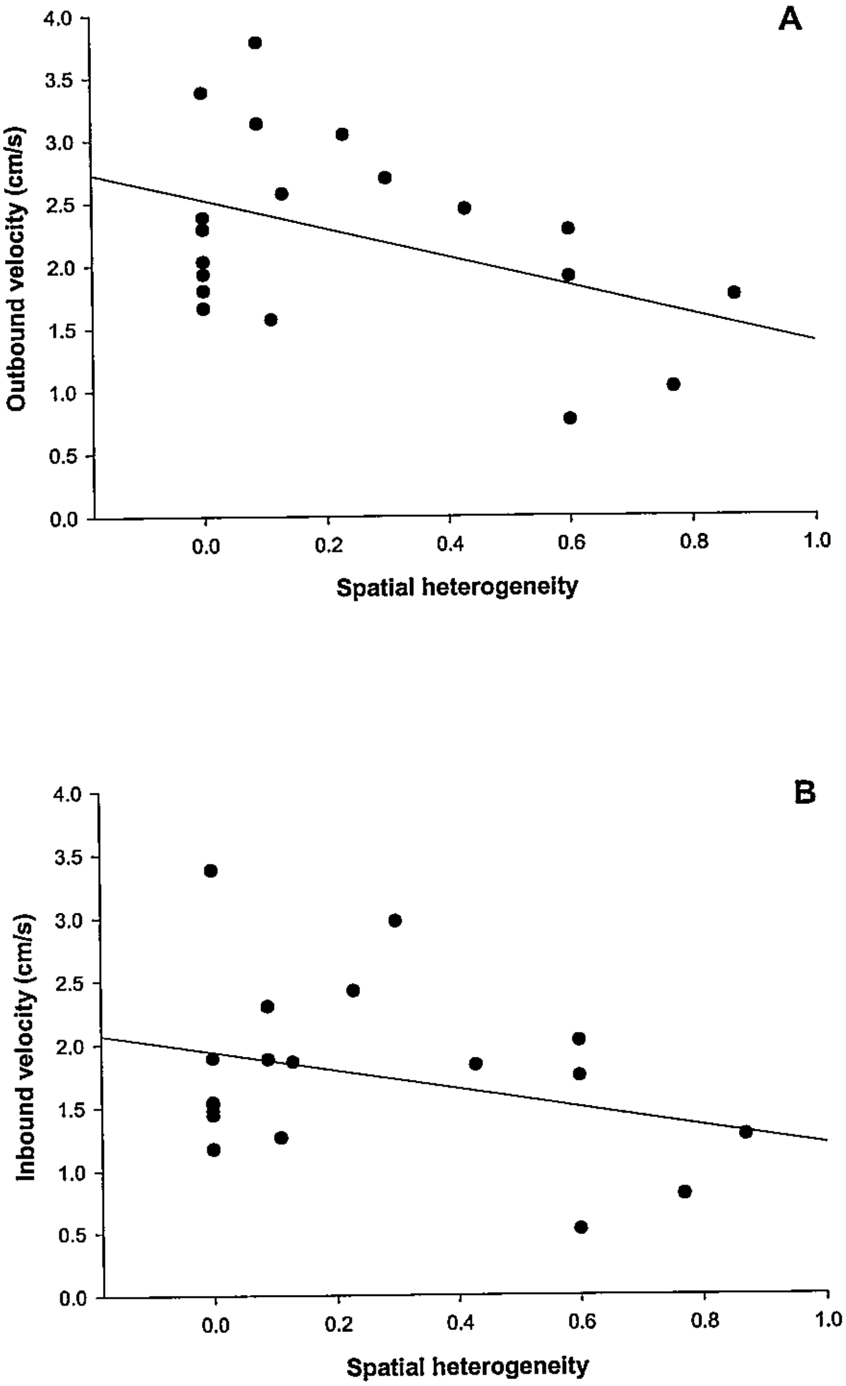

A
Outbound velocity (cm/s)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Spatial heterogeneity
B
Inbound velocity (cm/s)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Spatial heterogeneity

Table 1. Results of a two-way ANOVA for the effects of resource patch distance and food load and their interaction on the locomotion velocity of *Dorymyrmex goetschi* foragers. The soil temperature (T°) was utilized as covariate.

Source	df	SS	MS	F	P
Distance	1	2.069	2.069	7.339	0.011
Load	1	2.274	2.274	8.064	0.008
Distance x Load	1	0.371	0.371	1.316	0.259
Covariate (T°)	1	7.055	7.055	25.021	<0.0001
Error	33	9.306	0.282		

CAPÍTULO 3

How patch exploitation time and spatial heterogeneity affect locomotion and foraging in ants

ABSTRACT

The presence of novel resources in a heterogeneous landscape determines that the organisms experiment, throughout a temporary sequence, events of information acquisition which may improve the performance of foraging tasks. The spatial structure of habitats contains physical barriers that restrict the movements of individuals. Changes in locomotion performance and their effects on the foraging success of animals have been scarcely studied. These relationships were analyzed in the harvester ant *Dorymyrmex goetschi* (subfamily Dolichoderinae) under controlled laboratory conditions to eliminate the noise of other environment factors. In an experimental arena, I offered a food patch located at fixed distance from the nest entrance. Landscape heterogeneity was created using a constant number of similarly sized wooden cubes arranged in different types of spatial distribution. I video recorded the behavior of each colony and analyzed the following dependent variables: number of active foragers, number of head contacts per capita per inbound trip, path length by workers that transported a food load from the resource patch to the nest, time invested in these inbound travels, and the number of captured prey per colony. During the initial phase of patch exploitation, the number of foragers and prey captured were significantly lower than during the half and final phases. Landscapes with greater spatial heterogeneity increased travel time and diminished locomotion velocity. There was a positive and significant relationship between the number of foragers and head to head contacts. A multiple regression analysis revelead that greater antennal contacts and locomotion velocities increased prey removal. Therefore, in this study I documented a formal link between variables that characterize the movement paths of individuals and the foraging success of a colony. Successful foragers and information transfer between individuals would determine a collective work in food retrieval. The integration of multiple signals allows the generation of spatial navigation strategies, including guiding trajectories and the avoidance the physical barriers present in the landscape. Time saved during inbound trips could have an effect on the fitness of ant colonies.

Key words: information transfer, landscape, movement path, resource patch, *Dorymyrmex goetschi*

INTRODUCTION

The behavior of an animal is determined by its relation with the physical environment and its interactions with other organisms (Harper 1991). In an uncertain and changing environment, animals do not lack total information nor they are omniscient. Organisms continuously need to handle information to make more appropriate decisions (Stephens 1989; Koops 2004). For example, animals can reduce the amount of errors in their feeding behavior via experience and/or learning about the location and quality of resources, which finally affect the searching time and permanence in the patches (McNamara & Houston 1985, 1987; Lieberman 1993; Stephens 1993). The presence of novel resources in a heterogeneous habitat determines that organisms experiment throughout a temporary sequence events of acquisition, transfer and processing of information, all of which may improve the performance of foraging tasks (Giraldeau 1997; Rodriguez-Gironés & Vásquez 1997; Dukas 1998; Ydenberg 1998).

The spatial heterogeneity of the habitat can be expressed as the division of a certain space in favorable (patches) and unfavorable (areas between patches) sites (Southwood 1977). The structure of the landscape, understood as an abstract pattern of organization (e.g. different patch sizes) and spatial distribution (e.g. distance between patches) (McIntosh 1991), contains physical barriers that restrict the movement trajectories of individuals (Ims 1995; Wiens et al. 1995; McIntyre & Wiens 1999; Zollner & Lima 1999). Besides, the spatial heterogeneity experienced by an organism is the product of the interaction between the level of perceptual resolution of its environment and the spatial distribution of environmental constrains (Allen & Hoekstra 1991; Milne 1991). The movement paths of individuals that transport a food load in the matrix between a patch and a central place (e.g. nest), can vary during the exploitation time due to the accumulation of experience (e.g. Kolasa & Rollo 1991), and could affect the efficiency of resource removal.

During displacements, ants acquire information about the physical characteristics of the habitat and quality of novel resources (e.g. Adler & Gordon 1992; Roces 1993).

Specifically, foragers returning to the nest with food can stimulate the recruitment of their nestmates (e.g. Wilson & Hölldobler 1988; Roces 1990; Fourcassié & Traniello 1994). There are several sensorial signals (e.g. visual cues, vibratory signals, chemical marks, rate of encounters) by which ants transfer information (see Hölldobler 1999 for a review). For example, antennation between workers scouts and foragers allows decision making about feeding activities, through physiological and chemical mechanisms of recognition (e.g. Hölldobler 1999; Greene & Gordon 2003; Le Breton & Fourcassié 2004). This process follows simple decision rules (rules of thumb). For example, if a worker at a certain distance and time interval surpasses a threshold value of encounters with ants performing a given task (e.g. food transportation), this individual will initiate that activity (Wilson & Hölldobler 1988; Gordon1989; Gordon et al. 1993). On the other hand, structural characteristics of the substratum and a patchy distribution of resources restrict the movement and foraging success of ants (Crist & MacMahon 1991; Crist & Haefner 1994; Crist & Weins 1994). For example, an increase of the herbaceous cover diminishes locomotion speeds of harvester ants (e.g. Fewell 1988).

In this work I studied, under controlled conditions of laboratory, the changes in locomotion and foraging performance of a social insect that acquired information from its environment and was confronted to a given landscape spatial heterogeneity during the exploitation of a food patch. In a previous field study (Torres-Contreras & Vásquez, unpublished data) I evaluated these relationships in ants, but I have not found conclusive results. Laboratory experiments allow us to eliminate other environment factors that potentially can interfere locomotion and foraging behavior of ants. I asked the following questions: (1) Do activities of workers and resources removal vary with time? (2) Are movement paths affected by spatial heterogeneity? (3) Does antennation contacts between individuals produce changes in foraging efficiency? (4) Do movement paths have an effect on food retrieval? I predicted that: (i) during the final phase of patch exploitation, the number of foragers and captured prey will increase, (ii) landscapes with greater spatial heterogeneity will increase path length and travel time, (iii) a greater number of encounters among nestmates will increase foraging success, and, (iv) shorter path length and travel times will increase the number of prey captured. I discussed the relevance of the movements and feeding strategies in harvester ants that live in a spatially and temporally variable habitat.

METHODS

Study species and experimental arena

The locomotion and foraging behavior were studied in the species *Dorymyrmex goetschi* Menozzi 1935, which belong to subfamily Dolichoderinae (Snelling & Hunt 1975; Shattuck 1992). The workers of this species have red coloration in head and thorax, a black abdomen, and a body mass of 1.63 mg (Torres-Contreras & Vásquez 2004). These ants construct their nests in open spaces without tree or shrub vegetation. The entrance of the nest has characteristic earth hillocks produced by rubble removed from the interior by the ants. The daily activity of ants begins at dawn with a period of nest cleaning, proceeding afterwards with a period of exploratory and foraging activities. These activities are performed until soil temperature reaches 45° C. At this temperature the entrance of the nest is closed with vegetable material and activities ceases above ground (Torres-Contreras, personal observation). This species has been documented as belonging to the assembly of harvester ants (Medel and Vásquez 1994; Torres-Contreras 2001). An analysis of natural prey transported to the nest shows that this species incorporates insects to its diet in a percentage of 27-47% (Torres-Contreras, unpublished data).

During the summer 2002 I identified seven nests of *D. goetschi* in the Rio Clarillo National Reserve (33° 51' S, 70° 29' W), a lower Andes locality of central Chile located 45 km SE from Santiago, where this species constitutes one of the most common ants (Torres-Contreras, personal observation). I extracted the colonies by capturing all the workers that were carrying out tasks outside the nest, including cleaning, exploration, and/or foraging. After this, I carefully digged the soil to remove as much workers and larvae as possible, including the queen. The soil removal effort was standardized to two hours of excavation, and the excavation route consisted in following the workers that escaped through the tunnels, which communicated towards different chambers. I was able to reach a depth of 50 centimeters, to collect most of individuals and to capture the queen of the colony in 57% of the attempts. The number of workers, larvae, and presence of queen of each colony are shown in Table 1.

In the field, colonies were transferred to plastic boxes of 11.0 x 11.0 x 5.0 cm (length x width x height), supplied with four glass tubes of dimensions 1.2 x 7.5 cm (diameter x length) that contained cotton and water to provide humidity. In the laboratory, ants were acclimated during two weeks to their experimental nest and maintained at a constant temperature (25° C) with a 12:12 h light:dark photoperiod cycle. Each colony box was connected to the experimental arena (of dimensions 50.0 x 50.0 cm, length x width) by a vinyl tube (1.0 x 20.0 cm, diameter x length) that opened at the center of the arena from below. The floor of the arena was made of white melamine-coated wood (1.7 cm thick) and it was marked with a gride of 25 cells of 10 cm^2 each cell. The edges of the arena consisted of translucid Plexiglas walls of dimensions 15.0 x 0.5 cm (height x thick). These walls were covered with Fluon to avoid the flight of the ants. Artificial nests were maintained under a closed economy of feeding, that is, workers could obtain food only during the experimental treatments (e.g. MacNamara & Houston 1989).

Experimental design

In the field, *D. goetschi* transported natural loads with a mass of 0.97 ± 0.07 mg (mean ± SE, n= 506, range 0.002 – 13.542 mg; Torres-Contreras & Vásquez 2004). In the laboratory experiments I used compacted sugar microspheres as prey (5.61 ± 0.05 mg, mean ± SE, n = 100). Although the size of this experimental food was in the upper range of the natural prey distribution of these ants, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey variability was low or nil. Further, my observations revealed that prey handling was not affected by these food items (see Torres-Contreras & Vásquez 2004). I offered a food patch with 50 microspheres located at a distance of 20 cm from the nest entrance, and its position was changed at random with respect to the four cardinal points for each experimental treatment.

Landscape spatial heterogeneity was measured using the index of dispersion of patches (R_c) (modified from Forman & Godron 1986, and Forman 1995). Specifically, $R_c = 2\bar{r}\sqrt{p}$, evaluates the mean distance of an object to its closest neighbor ($\bar{r}$) and the density of objects (*p*) (Clark & Evans 1954; Pielou 1977). $R_c = 1$ means that objects are distributed at random, $R_c < 1$, that objects are clumped, and $R_c > 1$, that objects are distributed regularly. I used wooden cubes of 125 cm^3 as objects to modify environmental heterogeneity, and to restrict the movement of ants. An arena without obstacles was used as a control treatment. I used a constant number of 16 cubes that were distributed within the 25 cells of the experimental arena, and I counted the number of cubes that containning each cell. Following Wiens (1995) statistical criterion, that is, spatial variance > 0 to mean heterogeneity, and spatial variance = 0 to express homogeneity, it was possible to propose a "measurement of heterogeneity" (*sensu* Kolasa & Rollo 1991) for four landscapes, with the following decreasing order of spatial homogeneity: without obstacles ($s^2 = 0.00$) < objects distributed regularly ($s^2 = 0.24$) < objects distributed at random ($s^2 = 0.33$) < objects with distribution grouped ($s^2 = 0.57$).

An experiment with one colony per day was carried out, always at the same hour in the morning (10:00 h). The movement and feeding behavior of forager workers were video recorded with a Sony camera (model CCD-TRV 108) located 70 cm above the center of the experimental arena. This camera has fitted a Sony wide conversion lens 0.6x (model VCL-0637H). The behavior of colonies was recorded during 120 min. For analysis, the exploitation time was divided in three phases of 40 minutes (initial, half, final) with the objetive of evaluating changes in the feeding performance through time. After each experiment, the arena was cleaned with a solution of alcohol and water to eliminate any type of chemical mark left by the workers on the substratum. Videos were watched and the following dependent variables were measured: number of active foragers, number of head contacts per individual per trip, path length by workers that transported one food load (one microsphere in all cases) from the patch to the nest, time invested in inbound travels per ant, and number of captured prey per colony.

A high density of individuals has been correlated with high rates of antennal contacts per ant (e.g. Gordon 1996), and with improved decision making through of chemical mechanisms of recognition (e.g. Greene & Gordon 2003). I quantified every five minutes the number of foragers present in the experimental arena, and the number of head to head contacts that each worker experienced during its inbound trip. These contacts were used as estimates of information transfer. I followed the methodology and criterion used by Gordon et al. (1993) and Burd & Aranwela (2003) to determine an effective antennal contact between two ants. I quantified, minute by minute, the number of sugar microspheres captured by the colony, and considered a successful removal when a prey was introduced to the nest by a worker. The movements of individuals between the food patch and the nest were traced in transparent films put directly over a video monitor. These trajectories were scanned and converted to digital images. Path lengths were measured by using SigmaScan software (SPSS Inc.). This measurement is a simple description of the movement complexity exhibited by an organism (e.g. Turchin et al. 1991). I used measurements of distance and duration time of inbound trips to estimate locomotion velocities.

Statistical analysis

The data were analyzed using a protected multivariate analysis of variance for repeated measures. The method comprises a MANOVA to assess global effects, and repeated-measures ANOVAs if the MANOVA shows significant results (Scheiner 1993). In the ANOVA tests, colony was used as the sample unit, and hence data correspond to the mean of foragers per colony (the range of the number of workers was 4-42 for landscapes without objects; 8-28 for landscapes with uniform distribution of objects; 9-25 for landscapes with random distribution; and 11-25 for landscapes with contagious distribution). Simple linear regressions were used to analyze the relationships between colony size and the proportion of foragers, and between the number of foragers and the number of head to head contacts per capita. The effects of antennal contacts, path length, travel time, and locomotion velocity on the number of captured prey was analyzed with multiple linear regression. All tests were carried out with Statistica 6.0 software (StatSoft Inc.). Data shown correspond to the mean of the colonies, and the significance of the statistical tests was fixed to $\alpha = 0.05$. Data satisfied the assumptions of each test.

RESULTS

Multivariate analysis

The MANOVA showed overall significant main effect for exploitation phase and spatial heterogeneity, whereas the time x heterogeneity interaction did not have a significant effect (Table 2). I now show the analyses carried out separately for each dependent variable using two-way repeated-measures ANOVAs (see statistical analysis in methods).

Univariate analysis

The number of active foragers changed significantly with exploitation phase, but not with spatial heterogeneity or the interaction between both factors (Table 3). During the final phase of experimentation, the number of workers (25.57 ± 4.99, mean ± SE, n= 28) was a 16% greater that during the half phase (21.54 ± 5.17), and 50% greater than during the initial phase (12.75 ± 4.06) (Fig. 1a).

The number of prey captured by colony was significantly affected by exploitation phase, but not by spatial heterogeneity or the interaction between both factors (Table 3). During the initial phase the number of food items removed (1.86 ± 1.10, mean ± SE, n=

28) was 6.4 times less than during the half phase (13.79 ± 3.75), and 7.6 times less than during the final phase (16.00 ± 3.55) (Fig. 1b).

I found no effects of time phase (F= 1.398, df= 2, p= 0.284), heterogeneity (F= 0.949, df= 3, p= 0.438), nor of the interaction between both factors (F= 0.639, df= 6, p= 0.698), on path lengths by workers that transported a food load from the patch to the nest. The range of path lengths for time phase effect was 48.56-54.97 cm, that is, foragers covered 2.43-2.75 times the straight line distance from patch to the nest. The range of path lengths for heterogeneity effect was 47.44-56.46 cm, that is, foragers covered 2.37-2.82 times the straight line distance from patch to the nest.

The time invested by foragers during inbound trips was significantly affected by spatial heterogeneity, but not by exploitation phase and the interaction between both factors (Table 3). In landscapes with objects distributed at random the time invested (52.64 ± 5.09 s, mean ± SE, n= 21) was a 8% greater than in habitats with obstacles distributed uniformly (48.37 ± 4.23 s), 25% greater than in landscapes with clumped distribution (39.25 ± 3.90 s), and 34% greater than in habitats without obstacles (34.79 ± 5.26 s) (Fig. 2a).

The locomotion speed of foragers during inbound trips was significantly affected by spatial heterogeneity, but not by exploitation phase or the interaction between both factors (Table 3). In landscapes with obstacles distributed at random the velocity (1.06 ± 0.10 cm/s, mean ± SE, n= 21) was a 12% slower than in habitats with objects distributed uniformly (1.19 ± 0.09 cm/s), 26% slower than in landscapes with distribution grouped obstacles (1.34 ± 0.16 cm/s), and 43% slower than in habitats without objects (1.52 ± 0.12 cm/s) (Fig. 2b).

Regression analysis

There was a negative and significant relationship between colony size and percentage of foragers ($r^2 = 0.70$, $t = 3.43$, $p < 0.05$; Fig. 3a). On the other hand, there was a positive and significant relationship between the number of active foragers and the number of head contacts per ant per inbound trip ($r^2 = 0.44$, $t = 4.53$, $p < 0.001$; Fig. 3b). A multiple linear regression with forward-stepwise procedure (Table 4) revelead that antennal contacts and locomotion velocity have both a significantly effect on the number of captured prey, and that these variables explained a significant fraction (67%) of the variation in the foraging success of colonies (Table 5, and see Fig. 4). Considering the sign of the parameter estimates (slope), I suggest that high numbers of antennal contacts and locomotion velocities increase prey removal.

DISCUSSION

During the exploitation of a resource patch, there was an increment on the number of *D. goetschi* workers that carried out foraging tasks outside the nest, which can be associated to processes of information transference. Despite the scarce knowledge on the mechanisms of communication in ants of the subfamily Dolichoderinae, we suggest that the chemical sensors through antennation could be the main channel involved in the exchange of information among individuals (e.g. Hölldobler & Wilson 1990). When one ant contacts with their antenna the food transported by a nestmate returning to the nest, it can perceive, through the chemoreceptors located in the tips of these structures, the quality of the prey (e.g. Roces 1990; Le Breton & Fourcassié 2004). Furthermore, the arrival rate of successful foragers to the nest motivate further recruitment of workers (Roces & Núñez 1993). Thus, the rapidity whereupon the information is disseminated about new sources of food can have a significant adaptive value for the colony. Saving time in the execution of feeding tasks would allow a colony to monopolize food patches present in the habitat earlier (e.g. Roces 1993).

Colonies with a lower number of workers allocate a greater proportion of ants to foraging tasks. The colonies can modulate the maximum number of foragers outside the nest in accordance with their nutritional requirements (e.g. Jaffe & Deneubourg 1992, Mailleux et al. 2003). For example, young colonies (and of smaller size) need greater resource removal rates to assure growth, development, and reproduction (e.g. Bourke 1999). On the other hand, the level of activity exhibited by *D. goetschi* can be conditioned by the composition and predictability of resources. It has been documented that food items rich in carbohydrates present a regular rate of renewal and they provide an important energetic source, which determine a high rate of visits and route fidelity towards feeding sites (e.g. Fresneu 1985; Fourcassié & Traniello 1994).

The smaller number of prey removed during the initial phase of the patch exploitation would be determined by a temporary delay in the decision to accept previously unknow resources as suitable. In fact, in the field *D. goetschi* is essentially granivorous incorporating a great percentage of seeds and insects in its diet, but few food items rich in sugar (Torres-Contreras, unpublished data). In my laboratory experiments, independently of the spatial heterogeneity, food patches were discovered after 18.75 ± 2.48 minutes (mean ± SE, n= 28) from the entrance of workers to the experimental arena, but the first successful prey removal ocurred at 46.29 ± 2.90 min. This reflected the complexity of the signals present in the environment that are evaluated by scout ants. Later, the increase in resource removal is connected with a higher number of active foragers and antennal contacts. Encounters among workers during their inbound travel would allow information transfer to colony about the location and quality of the food patch, and thus the capture of a greater number of prey (see Detrain et al. 1999 for a review). These results corroborate field information on the effect of information processing in the foraging success of *D. goetschi* colonies (Torres-Contreras & Vásquez, unpublished data). Moreover, an effective exploitation of resources would require that foragers use several strategies for prey capture (e.g. Howard et al. 1996; Detrain et al. 1999). Thus, in some occasions *D. goetschi* foragers, like other species of the subfamily, can exhibit mass-recruitment (e.g. Oster & Wilson 1978; Beckers et al. 1989), and display a process of relay with indirect transfer of preys in dump sites (e.g. Ratnieks & Anderson 1999) during the return trips to the nest (Torres-Contreras, personal observation). In this way, the independent performance of individuals can be integrated in a collective work that allows the colony to make a more successful removal of resources (e.g. Detrain et al. 1990, Devigne & Detrain 2002).

Landscape spatial heterogeneity did not have an effect on food patch exploitation of *D. goetschi*, which could be due to the coarse grain of perception that these organisms have (*sensu* Levins 1968), allowing them to exploit resource patchiness distributed and located in sites with greater environmental rugosity (e.g. Kaspari & Weiser 1999; Farji-Brener et al. 2004). This capacity is higher in organisms that have extremities and body size proportionally smaller, due to the fact that they interact with the physical and structural characteristics of the habitat at spatial microscale (e.g. Farji-Brener et al. 2004).

Path length was not affected by exploitation time nor by spatial heterogeneity. This mean that trajectories were spatially marked by the individuals in the initial trips, possibly by means of chemical signals. The workers of *D. goetschi* would be able, as other species of Dolichoderinae, of marking the substratum with trail pheromones, which later are re-marked and used for guiding their return trips to the nest (e.g. Robertson et al. 1980). Nevertheless, in the field I found that the inbound travels of this species are more linear with the passing of time (Torres-Contreras & Vásquez, unpublished data). Besides, when I compared a route index that considers the ratio between path length and distance in straight line from the patch to the nest (20 cm), I found greater trajectories under laboratory conditions (2.37-2.82) than in field situations (1.47-1.78) (Torres-Contreras & Vásquez, unpublished data). This suggests that in the field *D. goetschi* foragers also use another type of signals during their inbound trips. For example, other species of ants use visual (e.g. walking near familiar marks, turn to the left or right of an obstacle) and celestial (e.g. orientation by using the azimuth of the sun, and the pattern of polarized light) signals during their movements (e.g. Collet et al. 1992; Wehner 1997; Akesson & Wehner 2002; Graham & Collet 2002). The integration of different signals allows the generation of strategies of spatial navigation, guiding trajectories and increasing the avoidance of physical barriers present in the landscape (e.g. Collet 1996; Wehner et al. 1996).

The relationship found in *D. goetschi* between variables that characterize movement paths and prey capture is a novel finding. Traditionally, locomotion and foraging behavior have been studied as independent events in the literature. Landscape ecology has studied the effects of spatial heterogeneity on the complexity of movement paths (e.g. With 1994; Wiens et al. 1995), but have not specified the stimulus that triggers movements, the changes that individual trajectories experience throughout time as result of information accumulation, and the influence that locomotion performance can have on other behaviors. On the other hand, models of optimal foraging have not considered explicitly the movement complexity displayed by the organisms in the matrix between food patches (see e.g. Charnov 1976, Orians and Pearson 1979, Pyke 1984), and, therefore, they have not analyzed the consequences of habitat heterogeneity on feeding performance. In this study, I documented a formal link between individual trajectories and foraging success of ant colonies. Specifically, I found that a greater locomotion velocity implies a greater number of removed resources.

On the other hand, landscapes with greater spatial heterogeneity increased travel time and reduced locomotion velocity. The magnitude of these variables can have consequences on the fitness of organisms, since a greater time investment outside the nest during a task may increase predation risk (e.g. Feener & Moss 1990), loss of thermal balance (e.g. Lighton & Bartholomew 1988), and/or the missing of information (e.g. Roces & Nuñez 1993). It has been documented that for ants it is not so important to maximize the energetic returns but to minimize time investment, and thus to maximize the net acquisition of resources in a certain period of time (e.g. Fewell 1988; Weier & Feener 1995). The greater number of captured prey by *D. goetschi* colonies when running speed was greater supports this proposal.

Optimal foraging in social insects is constrained by habitat characteristics and intrinsic factors of foragers and the colony (e.g. Detrain et al. 2000). Foraging strategies that maximize resource removal have an adaptative value, and can include more linear routes, shorter travel times, and recruitment of organisms (e.g. Harrison & Breed 1987; Fourcassié & Traniello 1994; Herbers & Choiniere 1996). In this study, I found that landscape spatial heterogeneity affects the movement paths of forager ants, information transfer among workers produce a collective work during the retrieval of food, and I could establish a formal relationship between two behaviors (locomotion and foraging) traditionally treated independently in the literature.

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LEGEND OF FIGURES

Figure 1: The effect of exploitation phase on the number of (**a**) active workers outside the nest and (**b**) captured prey by *D. goetschi* colonies. Values are mean of colonies, and different letters above points indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See Table 3 for details.

Figure 2: The effect of spatial heterogeneity (obstacles distribution type: W= without, U= uniform, R= random, C= contagious) on the (**a**) travel time and (**b**) locomotion velocity of *D. goetschi* foragers. Values are mean of colonies, and different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See Table 3 for details.

Figure 3: The relationship between (**a**) colony size and proportion of foragers, and between (**b**) the number of workers and the number of head to head contacts per capita per inbound trip in *D. goetschi* colonies. Values are mean of colonies; and the sample size was $n = 7$ and $n= 28$, respectively. See text for details.

Figure 4: The relationship between (**a**) number of antennal contacts per capita per inbound trip and captured prey ($r^2= 0.38$, $t = 3.98$, $p < 0.001$), and between (**b**) travel time and number of removed food items ($r^2= 0.14$, $t= 2.06$, $p= 0.0491$) by *D. goetschi* colonies. Values are mean of colonies; and the sample size was $n = 28$. See text for details.

Figure 1

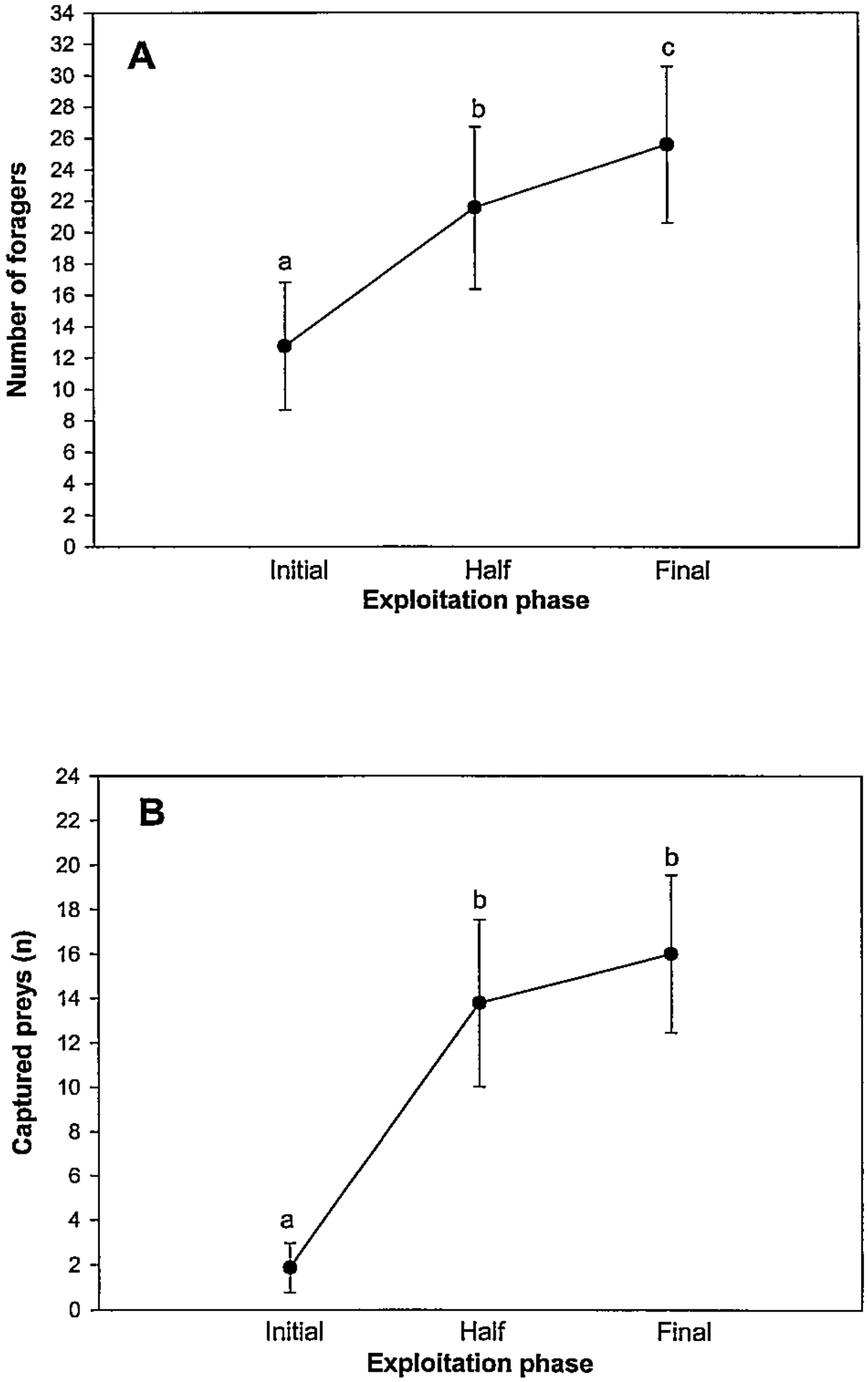

A
Number of foragers
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
a
b
c
Initial
Half
Final
Exploitation phase
B
Captured preys (n)
0
2
4
6
8
10
12
14
16
18
20
22
24
a
b
b
Initial
Half
Final
Exploitation phase

Figure 2

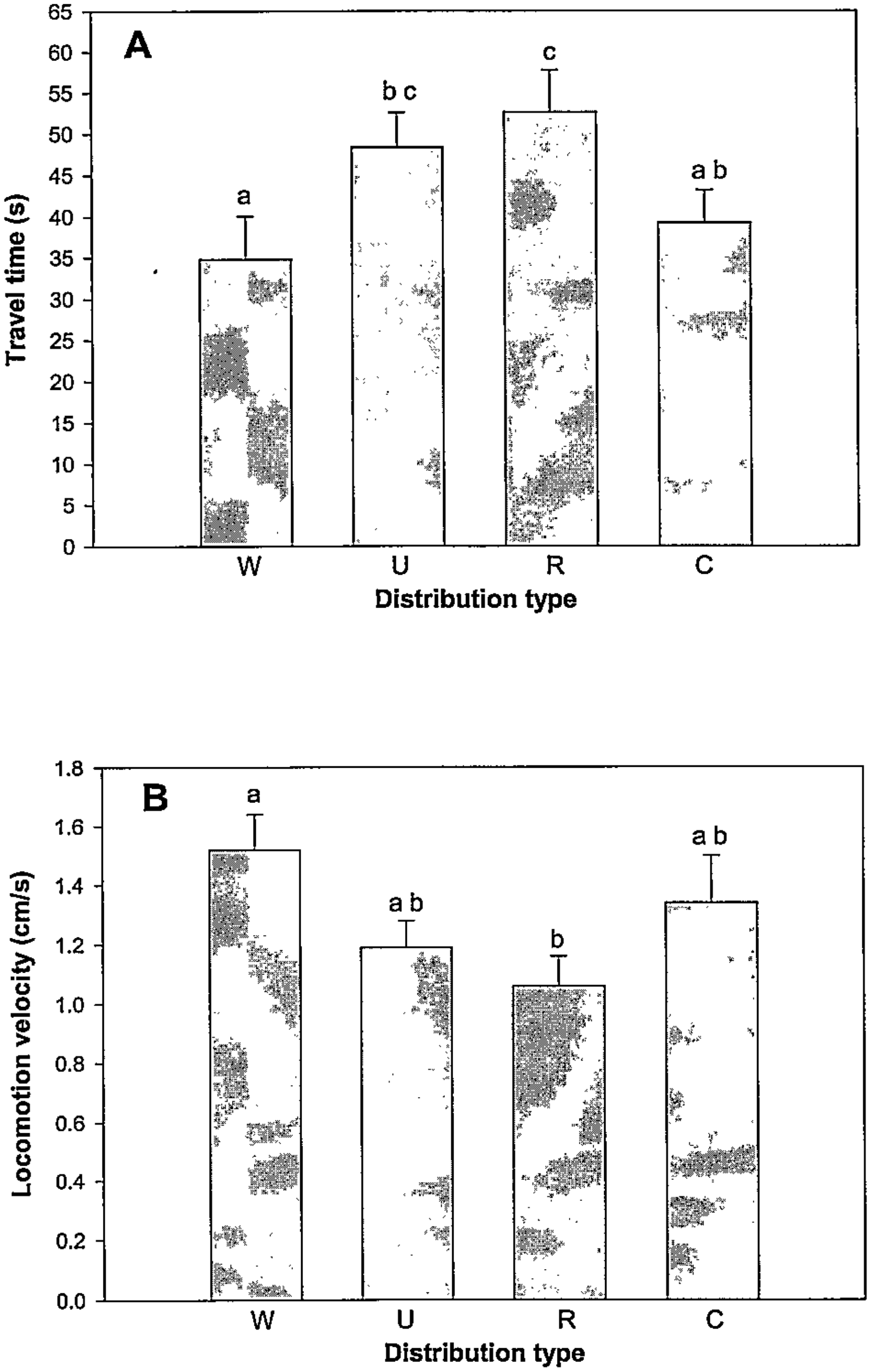
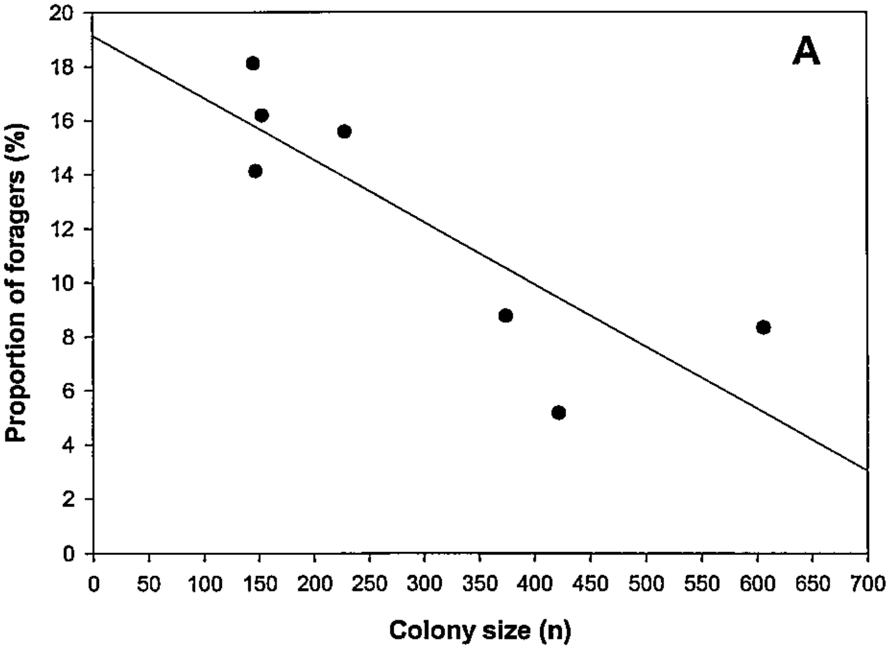

A
Travel time (s)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
a
b c
c
a b
W
U
R
C
Distribution type
B
Locomotion velocity (cm/s)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
a
a b
b
a b
W
U
R
C
Distribution type

Figure 3


A
Proportion of foragers (%)
0
2
4
6
8
10
12
14
16
18
20
Colony size (n)
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700

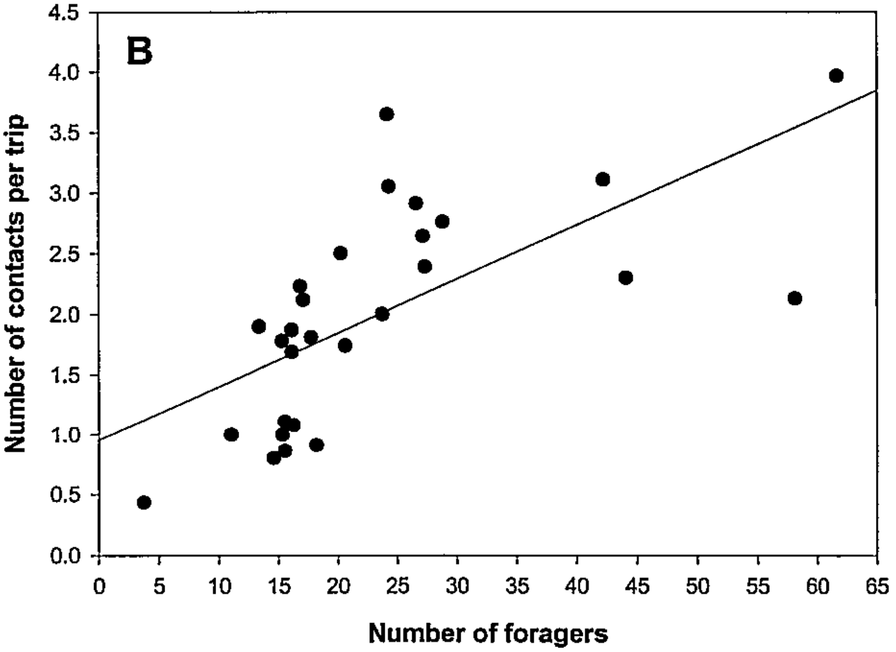

B
Number of contacts per trip
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
Number of foragers
0
5
10
15
20
25
30
35
40
45
50
55
60
65

Figure 4

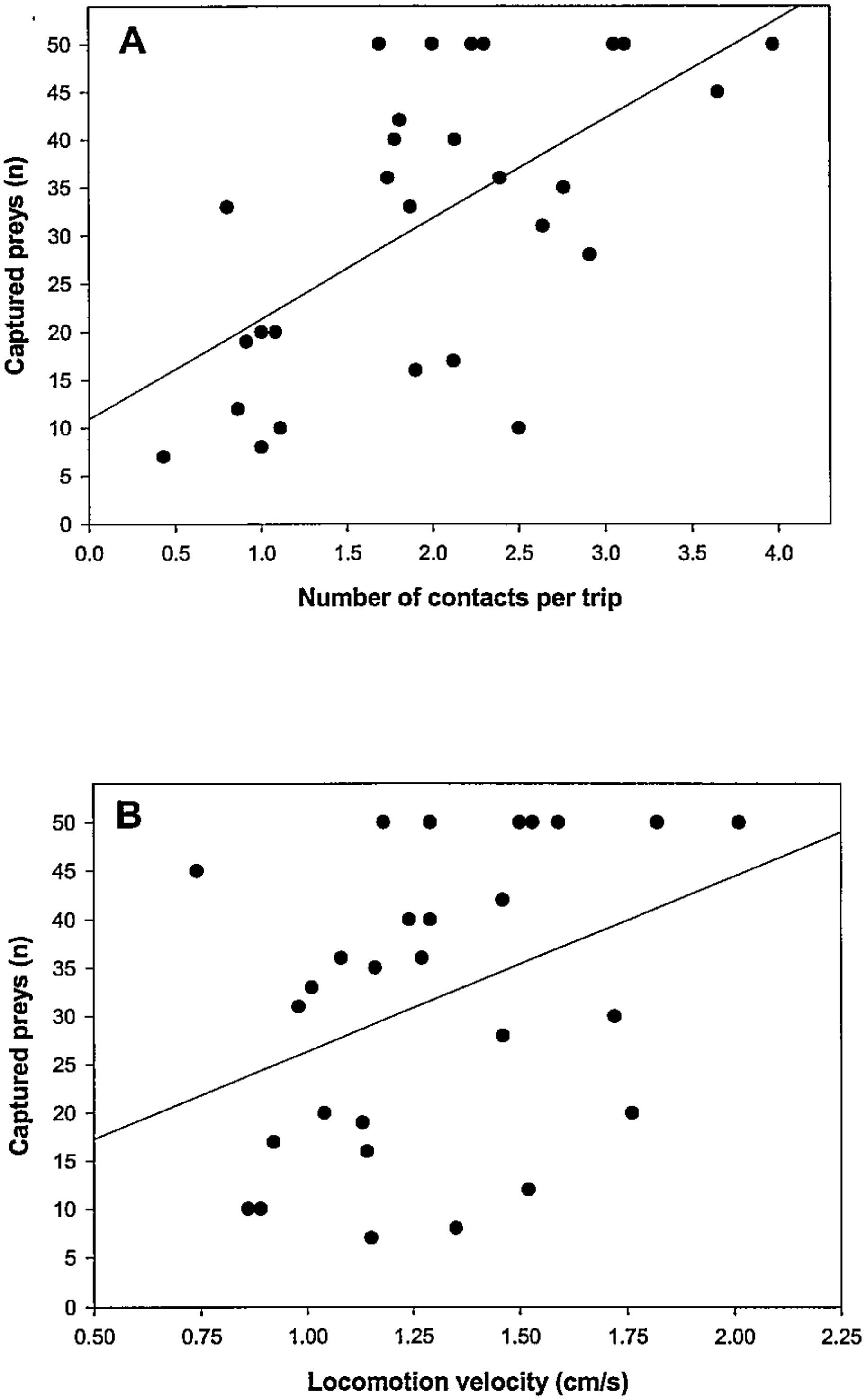

A
Captured preys (n)
0
5
10
15
20
25
30
35
40
45
50
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Number of contacts per trip
B
Captured preys (n)
0
5
10
15
20
25
30
35
40
45
50
0.50
0.75
1.00
1.25
1.50
1.75
2.00
2.25
Locomotion velocity (cm/s)

Table 1. Characteristics of *Dorymyrmex goetschi* colonies used in the different experimental treatments.

Colony	N° of workers	Presence of queen	N° of larvae	Maximum foragers (proportion of total)
1	422	Yes	2	21.75 ± 4.23 (5.15 %)
2	606	Yes	17	50.50 ± 10.08 (8.33 %)
3	147	Yes	10	20.75 ± 0.74 (14.12 %)
4	148	No	6	26.25 ± 4.64 (18.10 %)
5	374	No	19	32.75 ± 4.21 (8.76 %)
6	153	Yes	37	24.75 ± 2.48 (16.18 %)
7	228	No	12	35.50 ± 7.26 (15.57 %)

Table 2. MANOVA of exploitation time, spatial heterogeneity, and interaction effects on different dependent variables (number of foragers, path length, travel time, locomotion velocity, and captured preys) of the *D. goetschi* foragers.

Effect	Wilk's lambda	F	Numerator df	Denominator df	P
Time	0.580	4.255	10	136	< 0.0001
Heterogeneity	0.494	3.650	15	188	< 0.0001
T x H	0.711	0.811	30	274	0.749

Table 3. Results of a repeated-measured two-way ANOVA for the effects of exploitation time and spatial heterogeneity and their interaction on different dependent variables of the *Dorymyrmex goetschi* colonies.

Source	df	SS	MS	F	P
Number of foragers					
Time	2	2406.738	1203.369	191.869	<<0.0001
Heterogeneity	3	833.238	277.746	0.886	0.467
Time x Heterogeneity	6	234.402	39.067	1.915	0.105
Error	36	225.792	6.272		
Travel time					
Time	2	830.948	415.474	2.290	0.144
Heterogeneity	3	4218.336	1406.112	7.522	<0.01
Time x Heterogeneity	6	511.278	85.213	0.763	0.604
Error	36	4020.408	111.678		
Locomotion velocity					
Time	2	0.038	0.019	0.182	0.835
Heterogeneity	3	2.451	0.817	5.024	<0.05
Time x Heterogeneity	6	0.384	0.064	1.852	0.116
Error	36	1.260	0.035		
Captured preys					
Time	2	3240.666	1620.333	23.328	<0.001
Heterogeneity	3	225.57	75.190	1.224	0.330
Time x Heterogeneity	6	409.998	68.333	0.977	0.455
Error	36	2517.156	69.921		

Table 4. Summary of the results of forward-stepwise multiple linear regression on the effect of movement path variables and antennal contacts on the number of captured preys by *Dorymyrmex goetschi* colonies.

Step	Variable entered	F	Significance	r^2 ajusted	R^2 change
1	Head contacts	16.666	0.0004	0.391	0.391
2	Locomotion velocity	15.255	0.0007	0.622	0.231
3	Path length	3.351	0.0796	0.668	0.046

Table 5. Multiple linear regression model on the effect of movement path variables and antennal contacts on the number of captured preys by *Dorymyrmex goetschi* colonies.

Variable	Slope	Significance
Head contacts	10.146	<0.001
Locomotion velocity	24.049	<0.001
Path length	-6.274	0.079
Constant	-3.887	0.778

Regression Model Summary: $R^2 = 0.67$; $F_{3,24} = 16.09$; $p < 0.00001$

CAPÍTULO 4

Influence of information transfer, landscape heterogeneity and movement path on foraging success in two species of *Camponotus* ants

ABSTRACT

Information acquired from the environment can improve the performance of different behavioral tasks. Landscape spatial heterogeneity restricts the trajectories of animals because physical barriers make movement more difficult. Nevertheless, studies up to date have not linked the stimulus that trigger movement, the changes in complexity that trajectories experience throughout time as result of information accumulation, and the influence of locomotion performance on other behaviors. In relation to the last point, models of optimal foraging have not considered explicitly the movement complexity displayed by the organisms in the matrix between resource patches, and, therefore, they have not analyzed their consequences on feeding performance. I studied these relationships in the carpenter ants *Camponotus morosus and C. chilensis* (subfamily Formicinae) under controlled laboratory conditions. In an experimental arena, I offered a food patch located at a fixed distance from the nest entrance. Landscape heterogeneity was created using a constant number of similarly sized wooden cubes arranged in different types of spatial distribution. I video recorded the behavior of each colony and analyzed the following dependent variables: number of active foragers, number of head contacts per capita per inbound trip, path length by workers that transported a food load from the food patch to the nest, time invested in these inbound travels, and the number of captured prey per colony. During the final phase of patch exploitation, locomotion velocity of *C. chilensis* foragers was significantly greater than during the initial and half phase. Further, in this species the clumped distribution of obstacles increased locomotion speed. *Camponotus morosus* removed a greater number of preys during the initial phase, however, *C. chilensis* captured more food items during the half phase. In both species there was a positive and significant relationship between the number of foragers and the number of head to head contacts. A multiple regression analysis revealed that in both species a greater number of antennal contacts increases the removal of prey; but only in *C. morosus* I found that a shorter travel time increases the colected food. Therefore, this study documented a formal link between variables that characterize the movement paths of individuals and the foraging success of a colony. The return of successful foragers and information transfer between individuals would determine a mass-recruitment and collective work in food retrieval. The integration of multiple signals allows the generation of strategies of spatial navigation, guiding trajectories and increasing the avoidance the physical barriers present in the landscape. Time saving during inbound trips could have an effect on the fitness of ant colonies.

Key words: antennal contact, physical obstacle, path length, resource patch, carpenter ants

INTRODUCTION

When searching for and when carrying food, ants exhibit different movement patterns. The shape of these displacements is influenced by the physical barriers of the landscape. Habitats with greater spatial heterogeneity of barriers produce complex trajectories, that is, tracks with a high superimposition of paths resulting in a larger covered area (Fourcassié et al. 1992; Wiens et al. 1995). Specifically, structural characteristics of the substratum and patchy distribution of resources restrict the movement and foraging success of ants (Crist and MacMahon 1991; Crist and Haefner 1994; Crist and Weins 1994). For example, an increase of the herbaceous cover diminishes locomotion speeds of harvester ants (e.g. Fewell 1988). On the other hand, during their displacements, ants acquire information about the physical characteristics of the habitat and about the quality of novel resources (e.g. Adler and Gordon 1992; Roces 1993). Furthermore, foragers returning to the nest with food can stimulate the recruitment of their nestmates (e.g. Wilson and Hölldobler 1988; Roces 1990; Fourcassié and Traniello 1994). There are several signals (e.g. visual cues, vibratory signals, chemical marks, rate of encounters) by which ants transfer information to conspecifics (see Hölldobler 1999 for a review). For example, antennation between workers scouts and foragers allows decision making about feeding activities, through physiological and chemical mechanisms of recognition (e.g. Hölldobler 1999; Greene and Gordon 2003; Le Breton and Fourcassié 2004). This process follows simple decision rules (rules of thumb). For example, if a worker at a certain distance and time interval surpasses a threshold value of encounters with ants performing a given task (e.g. food transportation), this individual will initiate that activity (Wilson and Hölldobler 1988; Gordon1989; Gordon et al. 1993).

Ants can exploit a food source by means of solitary and/or social foraging. The last behavior involves a cooperative work between individuals, where workers interchange information, resulting in recruitment towards the patch, and an efficient resource removal (e.g. Oster and Wilson 1978; Hölldobler and Wilson 1990). Ant species present a diversity of foraging strategies and information processing mechanisms. For example, ants of genus *Camponotus* exhibit solitary foraging with diffuse recruitment of individuals and/or recruitment in tandem running (Oster and Wilson 1978). It has been documented that *Camponotus* species acquire information from its surroundings by means of vibrational signals, visual orientation and/or secreted trail pheromones (Hölldobler and Wilson 1990). Here, I report the interrelated influence of information transfer through antennation, landscape heterogeneity, and movement path on prey capture in the species *Camponotus morosus* (body weight of 7.52 ± 0.66 mg, mean ± SE, n = 10) and *C. chilensis* (6.58 ± 0.38 mg, n = 10). These ants are abundant and have a wide distribution in central Chile (Snelling and Hunt 1975); they construct their nest under rocks, they have a bimodal activity period, and are generalist harvesters (e.g. Grez et al. 1988; Ipinza-Regla et al. 1988; Torres-Contreras, personal observation).

I studied the effects of antennal contacts (information transfer), spatial distribution of obstacles, and both time and path length of inbound trips on the exploitation of a novel resource patch in *C. morosus* and *C. chilensis*. In order to evaluate the influence of these factors and their interactions on the foraging performance of these ants I carried out experiments under controlled laboratory conditions. Therefore, I could eliminate other environment factors that potentially interfere locomotion and foraging behavior. Treatments consisted in different spatial arrays of objects in the landscape, and I analyzed how these influenced the activity of foragers during food patch exploitation. I predicted that greater information transfer, lower landscape heterogeneity and more linear trajectories will increase removal rate of resources. In this study I related aspects of microlandscape ecology with animal behavior, establishing a formal connection between two behaviors (locomotion performance and foraging success) traditionally treated independently in the literature.

METHODS

Collection of ant colonies, and experimental arena

During the autumn 2002 I identified five nests of *C. morosus* and six of *C. chilensis* in the Rio Clarillo National Reserve (33° 51' S, 70° 29' W), a lower Andes locality of central Chile situated 45 km SE from Santiago, where these species constitute two of the most common ants (Torres-Contreras, personal observation). I extracted the colonies by raising a rock and capturing with forceps all the workers, soldiers, and winged individuals that were on the surface. After this, I carefully dug the soil to remove as much workers and larvae as possible, including the queen. The soil removal effort was standardized to two hours of excavation, and the excavation route consisted in following the workers that escaped through the tunnels, which communicated towards different chambers. I was able to reach a depth of 50 centimeters, and to collect most of individuals. The number of captured workers by colony ranged between 100-200 individuals.

In the field, colonies were transferred to plastic boxes of 50.0 x 20.0 x 10.0 cm (length x width x height), supplied with four glass tubes of 1.5 x 16.0 cm (diameter x length) that contained cotton and water to provide humidity. In the laboratory, ants were acclimated during two weeks to their experimental nest and maintained at a constant temperature (25° C) with a 12:12 h light:dark photoperiod cycle. Each colony box was connected to the experimental arena (of dimensions 50.0 x 50.0 cm, length x width) by a vinyl tube (1.0 x 20.0 cm, diameter x length) that opened at the center of the arena from below (see Fig. 1). The floor of the arena was made of white melamine-coated wood (1.7 cm thick) and it was marked with a grid of 25 cells of 10 cm^2 each cell. The edges of the arena consisted of translucid Plexiglas walls of 15.0 x 0.5 cm (height x thick). These walls were covered with Fluon to avoid the flight of the ants. Artificial nests were maintained under a closed economy of feeding, that is, workers could obtain food only during the experimental treatments (e.g. MacNamara and Houston 1989).

Experimental design

During the experiments I used compacted sugar microspheres as prey (5.61 ± 0.05 mg, mean ± SE, n = 100). Although the size of this experimental food can be in the upper range of the natural prey distribution of these ants species, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey variability was low or nil. Further, my observations revealed that prey handling was not affected by these food items (see Torres-Contreras & Vásquez 2004). I offered a food patch with 50 microspheres located at a distance of 20 cm from the nest entrance, and its position was changed at random with respect to the four cardinal points for each experimental treatment.

Landscape spatial heterogeneity was measured using the index of dispersion of patches (R_c) (modified from Forman and Godron 1986; and Forman 1995). Specifically, $R_c = 2\bar{r}\sqrt{p}$, evaluates the mean distance of an object to its closest neighbor ($\bar{r}$) and the density of objects (p) (Clark and Evans 1954; Pielou 1977). $R_c = 1$ means that objects are distributed at random, $R_c < 1$, that objects are clumped, and $R_c > 1$, that objects are distributed regularly. I used wooden cubes of 125 cm^3 as objects to modify environmental heterogeneity, and to restrict the movement of ants. An arena without obstacles was used as a control treatment. I used a constant number of 16 cubes that were distributed within the 25 cells of the experimental arena, and I counted the number of cubes that containing each cell. Following Wiens (1995) statistical criterion, that is, spatial variance > 0 to mean heterogeneity, and spatial variance = 0 to express homogeneity, it was possible to propose a "measurement of heterogeneity" (*sensu* Kolasa and Rollo 1991) for four landscapes, with the following decreasing order of spatial homogeneity: without obstacles ($s^2 = 0.00$) < objects distributed regularly ($s^2 = 0.24$) < objects distributed at random ($s^2 = 0.33$) < objects with distribution grouped ($s^2 = 0.57$).

An experiment with one colony per day was carried out, always at the same hour in the morning (10:00 h). The movement and feeding behavior of forager workers were video recorded with a Sony camera (model CCD-TRV 108) located 70 cm above the center of the experimental arena. This camera has fitted a Sony wide conversion lens 0.6x (model VCL-0637H). The behavior of colonies was recorded during 120 min. For analysis, the exploitation time was divided in three phases of 40 minutes (initial, half, final) with the objective of evaluating changes in the feeding performance throughout time. After each experiment, the arena was cleaned with a solution of alcohol and water to eliminate any chemical mark left by the workers on the substratum. Videos were watched and the following dependent variables were measured: number of active foragers, number of head contacts per individual per trip, path length by workers that transported one food load (one microsphere in all cases) from the patch to the nest, time invested in inbound travels per ant, and the number of captured prey per colony.

A high density of individuals has been correlated with high rates of antennal contacts per ant (e.g. Gordon 1996), and with improved decision making through of chemical mechanisms of recognition (e.g. Greene and Gordon 2003). I quantified every five minutes the number of foragers present in the experimental arena, and the number of head to head contacts that each worker experienced during its inbound trip. These contacts were used as estimates of information transfer. I followed the methodology and criterion used by Gordon et al. (1993) and Burd and Aranwela (2003) to determine an effective antennal contact between two ants. I quantified, minute by minute, the number of sugar microspheres captured by the colony, and considered a successful removal when a prey was introduced to the nest by a worker. The displacements of individuals between the food patch and the nest were traced in transparent films put directly over a video monitor. These trajectories were scanned and converted to digital images. Path lengths were measured by using SigmaScan software (SPSS Inc.). This measurement is a simple description of the movement complexity exhibited by an organism (e.g. Turchin et al. 1991). I used measurements of distance and duration time of inbound trips to estimate locomotion velocities.

Statistical analysis

The data were analyzed using a protected multivariate analysis of variance for repeated measures. The method comprises a MANOVA to assess global effects, and repeated-measures ANOVAs if the MANOVA shows significant results (Scheiner 1993). In the ANOVA test, colony was used as the sample unit, and hence data corresponded to the mean of foragers per colony (the range of the number of workers was 6-30 in *C. morosus* and 4-26 in *C. chilensis* for landscapes without objects; 5-22 and 7-16 for landscapes with uniform distribution of objects; 7-26 and 6-21 for landscapes with contagious distribution; and 4-29 and 5-21 for landscapes with random distribution, respectively). Simple linear regressions were used to analyze the relationships between the number of foragers and the number of head to head contacts per capita. The effects of antennal contacts, path length, travel time, and locomotion velocity on the number of captured prey was analyzed with multiple linear regression. All tests were carried out with Statistica 6.0 software (StatSoft Inc.). Data shown correspond to the mean of the colonies, and the significance of the statistical tests was fixed to $\alpha = 0.05$. Data satisfied the assumptions of each test.

RESULTS

Multivariate analysis

The MANOVA showed overall significant main effect of exploitation time, species, and a time x species interaction (Table 1A). The analysis carried out separately for each dependent variable using two-way repeated-measures ANOVAs (see statistical analysis in methods) showed a significant effect on locomotion velocity and captured prey (Table 1B). I now show the ANOVAs test for each species.

Univariate analysis

In both species the number of active foragers, path lengths, and travel times were not significantly affected by exploitation phase, spatial heterogeneity, species, nor by the interactions between these factors. In *C. morosus* the range of active foragers was 13.07-18.80 and in *C. chilensis* was 12.32-16.42; the path length in *C. morosus* ranked between 57.40-74.05 cm and in *C. chilensis* between 51.38-69.72 cm; the travel time in *C. morosus* ranked between 18.36-22.16 s and in *C. chilensis* between 20.58-24.81 s.

In *C. chilensis* the locomotion speed of foragers during inbound trips was significantly affected by exploitation phase and spatial heterogeneity, but not by the interaction between both factors (Table 2). During the final phase of experimentation, locomotion velocity (3.14 ± 0.11 cm/s, mean ± SE, n= 24) was 10% greater than during the half phase (2.83 ± 0.10), and 16% greater than during the initial phase (2.63 ± 0.09) (Fig. 2a). In landscapes with clumped distribution of obstacles velocity (3.11 ± 0.13 cm/s, mean ± SE, n= 18) was 4% greater than in habitats with objects distributed at random (3.00 ± 0.14), 13% greater than in landscapes with obstacles distributed uniformly (2.71 ± 0.08), and 15% greater than in habitats without objects (2.64 ± 0.12) (Fig. 2b). On the other hand, in *C. morosus* locomotion velocity was not affected by exploitation phase, spatial heterogeneity, nor by the interaction between both factors (Table 2). The range of speed for this species was 3.09-3.48 cm/s.

In *C. morosus* the number of prey captured by colony was significantly affected by exploitation phase, but not by spatial heterogeneity or the interaction between both factors (Table 2). During the initial phase, the number of food items removed (16.85 ± 3.18, mean ± SE, n= 20) was 1.6 times greater than during the half phase (10.55 ± 1.78), and 5.0 times greater than during the final phase (3.40 ± 0.97) (Fig. 3a). Similarly, in *C. chilensis* the number of prey captured by colony was significantly affected by exploitation phase, but not by spatial heterogeneity or the interaction between both factors (Table 2). During the half phase, the number of food items removed (16.58 ±

2.18, mean ± SE, n= 24) was 2.0 times greater than during the final phase (8.33 ± 1.17), and 2.6 times greater than during the initial phase (6.42 ± 1.51) (Fig. 3b).

Regression analysis

In *C. morosus* there was a positive and significant relationship between the number of active foragers and the number of head contacts per ant per inbound trip (r^2= 0.66, t = 5.97, $p < 0.0001$; Fig. 4a). A similar result was found in *C. chilensis* (r^2= 0.59, t = 5.69, $p < 0.0001$; Fig. 4b). A multiple linear regression with forward-stepwise procedure (Table 3A) revelead that antennal contacts in *C. chilensis* have a significantly effect on the number of captured prey, and that this variable explained a significant fraction (44%) of the variation in the foraging success of colonies (Table 3B, and see Fig. 5b). Considering the sign of the parameter estimates (slope), I suggest that high numbers of antennal contacts increase prey removal. Similarly, in *C. morosus* a multiple linear regression with forward-stepwise procedure (Table 4A) revelead that antennal contacts and travel time have both a significantly effect on the number of captured prey, and that these variables explained a significant fraction (51%) of the variation in foraging success of colonies (Table 4B, and see Fig. 5a). Considering the sign of the parameter estimates, I suggest that high numbers of antennal contacts and shorter travel times increase prey removal.

DISCUSSION

The high level of activity exhibited by *C. morosus* and *C. chilensis* from the beginning of patch exploitation can be a consequence of the nutritional state of colonies and, therefore, the feeding motivation of individual foragers (e.g. Josens and Roces 2000). In fact, *Camponotus* colonies deprivated of food resources during one to two weeks, exhibit a massive recruitment during the first two hours after allowing access to food (e.g. Josens and Roces 2000). Further, the composition and predictability of resources can condition recruitment levels. Food items rich in carbohydrates present a regular rate of renewall and they provide an important energetic source, which determine a high rate of visits and route fidelity towards feeding sites (e.g. Fresneu 1985; Fourcassié and Traniello 1994, Schilman and Roces 2003).

Independently of the spatial heterogeneity, food patches were discovered after 87.50 ± 10.43 seconds (mean ± SE, n = 20) from the entrance of *C. morosus* foragers to the experimental arena. In *C. chilensis*, workers discovered the food after 150.00 ± 15.64 seconds (n = 24). The early discovery of resources allows a quick information transfer among workers inside the colony, and this resulted in a more or less constant number of workers carrying out foraging tasks. The main channels of communication in ants are the chemical sensors through antennation (e.g. Hölldobler and Wilson 1990). When one ant contacts with their antenna the food transported by a nestmate returning to the nest, it can perceive, through the chemoreceptors located in the tips of these structures, the quality of the prey (e.g. Roces 1990; Le Breton and Fourcassié 2004). Furthermore, the arrival rate of successful foragers to the nest motivates further recruitment of workers (Roces and Nuñez 1993). Thus, the rapidity whereupon the information is disseminated about new sources of food can have a significant adaptive value for the colony. Saving time in the execution of feeding tasks would allow a colony to monopolize food patches present in the habitat earlier (e.g. Roces 1993).

Path length was not affected by exploitation time nor by spatial heterogeneity. This means that trajectories were spatially marked by individuals in the initial trips, possibly by means of chemical signals. Different species of *Camponotus* mark the substratum with trail pheromones, which later are re-marked and used for guiding their return trips to the nest (e.g. Bestmann et al. 1995, Ubler et al. 1995, Haak et al. 1996, Kohl et al. 2001, 2003). It is possible also that *Camponotus* ants can use chemical emanations of the food for guiding their trajectories towards patches, following the "topochemical sense" hypothesis (e.g. Helmy and Jander 2003). On the other hand, a route index that considers the ratio between path length and distance in straight line from the patch to the nest (20 cm), shows values between 2.87-3.70 for *C. morosus* and 2.57-3.49 for *C. chilensis*. These values coincide with sinusoidal and complex trajectories documented for *Camponotus* workers during searching and foraging (e.g. Ganeshaiah and Veena 1988, Veena and Ganeshaiah 1991), and suggests that in the field *Camponotus* foragers use another type of signals during their inbound trips. For example, other species of ants use visual (e.g. turn to the left or right of an obstacle) and celestial (e.g. orientation by using the pattern of polarized light) signals during their displacements (e.g. Collet et al. 1992; Wehner 1997; Akesson and Wehner 2002; Graham and Collet 2002). In this way, it is possible that the increase in locomotion velocity of *C. chilensis* foragers during the final phase of patch exploitation involves learning about characteristics of the landscape. Faster running speed in habitats with clumped distribution of obstacles supports this assertion, whereas ants use walking near familiar marks. The integration of different signals allows the generation of strategies of spatial navigation, guiding trajectories and increasing the avoidance the physical barriers present in the landscape (e.g. Collet 1996; Wehner et al. 1996).

The greater number of prey removed by *C. morosus* during the initial phase of patch exploitation may be determined by the first successful removal that occurred at 16.05 ± 1.49 min (mean ± SE, n = 20). In contrast, the first removal in *C. chilensis* occurred at 29.50 ± 3.15 min (n = 24), determining a greater capture of food items during the half phase of experimentation. The differences between both species could originate from the fact that *C. morosus* moves exclusively on the ground surface (while *C. chilensis* also occupies shrubs and trees), is relatively more active at high temperatures, and uses more open spaces without vegetation (Torres-Contreras, personal observation). Besides, the increase in resource removal is connected with a higher number of active foragers and antennal contacts. Encounters between workers during their inbound travel would allow information transfer to colony members about the location and quality of the food patch, hence making possible a greater capture of prey (see Detrain et al. 1999 for a review). Moreover, an effective exploitation of resources would require that the foragers use several strategies for prey capture. Thus, in some occasions *Camponotus* foragers can exhibit mass-recruitment (e.g. Oster and Wilson 1978; Hölldobler and Wilson 1990), during the return trips to the nest (Torres-Contreras, personal observation). In this way, the independent performance of individuals can be integrated in a collective work that allows the colony to make a more successful removal of resources (e.g. Detrain et al. 1990, Devigne and Detrain 2002).

Landscape spatial heterogeneity did not have an effect on food patch exploitation of *C. morosus* and *C. chilensis*, which could be due to the coarse grain of perception that these organisms have (*sensu* Levins 1968), allowing them to exploit resource patchiness located in sites with greater environmental rugosity (e.g. Kaspari and Weiser 1999; Farji-Brener et al. 2004). This capacity is higher in organisms that have extremities and body size proportionally smaller, due to the fact that they interact with the structural characteristics of the habitat at spatial microscale (e.g. Farji-Brener et al. 2004).

The relationship found in *C. morosus* between travel time and prey capture is a novel finding. Traditionally, locomotion and foraging behavior have been studied as independent events in the literature. Landscape ecology has studied the effects of spatial heterogeneity on the complexity of movement paths (e.g. With 1994; Wiens et al. 1995), but have not specified the stimulus that triggers movements, the changes that individual trajectories experience through time as result of information accumulation, and the influence that locomotion performance can have on other behaviors. On the other hand, models of optimal foraging have not considered explicitly the movement complexity displayed by organisms in the matrix between food patches (see e.g. Charnov 1976, Orians and Pearson 1979, Pyke 1984), and, therefore, they have not analyzed the consequences of habitat heterogeneity on feeding performance. In this study, I documented for *C. morosus* a formal link between individual trajectories and foraging success. Specifically, I found that shorter travel times during inbound trips results in a greater number of removed resources. A greater investment of time outside the nest for a given task can have consequences on the fitness of organisms due to an increase in predation risk (e.g. Feener and Moss 1990), loss of thermal balance (e.g. Lighton and Bartholomew 1988), and/or the missing of information (e.g. Roces and Nuñez 1993). It has been documented that for ants it is not so important to maximize the energetic returns but to minimize time investment, and thus to maximize the net acquisition of resources in a certain period of time (e.g. Fewell 1988; Weier and Feener 1995). The greater number of captured prey by *C. morosus* colonies when travel time of foragers was shorter supports this proposal.

Optimal foraging in social insects is constrained by habitat characteristics and intrinsic factors foragers and the colony (e.g. Detrain et al. 2000). Foraging strategies that maximize resource removal have an adaptative value, and can include more linear routes, shorter travel times, and recruitment of organisms (e.g. Harrison and Breed 1987; Fourcassié and Traniello 1994; Herbers and Choiniere 1996). In this study, I found that information transfer among workers produce a collective work during the retrieval of food, and I could establish a formal relationship between two behaviors (locomotion and foraging) traditionally treated independently in the literature.

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LEGEND OF FIGURES

Figure 1: Experimental set-up. Each artificial nest was connected to one experimental arena that contained a constant number of obstacles with different distribution type and a food patch located at a fixed distance from the net entrance. The locomotion and foraging behavior of the colonies were video-recorded. See text for details.

Figure 2: The effect of exploitation phase (**a**) and spatial heterogeneity (**b**) on locomotion velocity of *C. chilensis* foragers. Distribution type of obstacles is: W= without, U= uniform, R= random, C= contagious. Values are mean of colonies, and different letters above points and bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See Table 2 for details.

Figure 3: The effect of exploitation phase on the number of captured prey by *C. morosus* (**a**) and *C. chilensis* (**b**) colonies. Values are mean of colonies, and different letters above points indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See Table 2 for details.

Figure 4: The relationship between the number of workers and the number of head to head contacts per capita per inbound trip in *C. morosus* (**a**) and *C. chilensis* (**b**) colonies. Values are mean of colonies, and the sample size was $n = 20$ and $n = 24$, respectively. See text for details.

Figure 5: The relationship between the number of antennal contacts per capita per inbound trip and the number of captured prey by *C. morosus* ($r^2= 0.21$, $t = 2.17$, $p < 0.05$) (**a**) and *C. chilensis* ($r^2= 0.36$, $t = 3.55$, $p < 0.01$) (**b**) colonies. Values are mean of colonies, and the sample size was $n = 20$ and $n = 24$, respectively. See text for details.

Figure 6: The relationship between travel time of foragers and the number of removed food items by *C. morosus* colonies ($r^2= 0.39$, $t= 3.37$, $p < 0.01$). Values are mean of colonies, and the sample size was $n = 20$ and $n = 24$, respectively. See text for details.

Figure 1

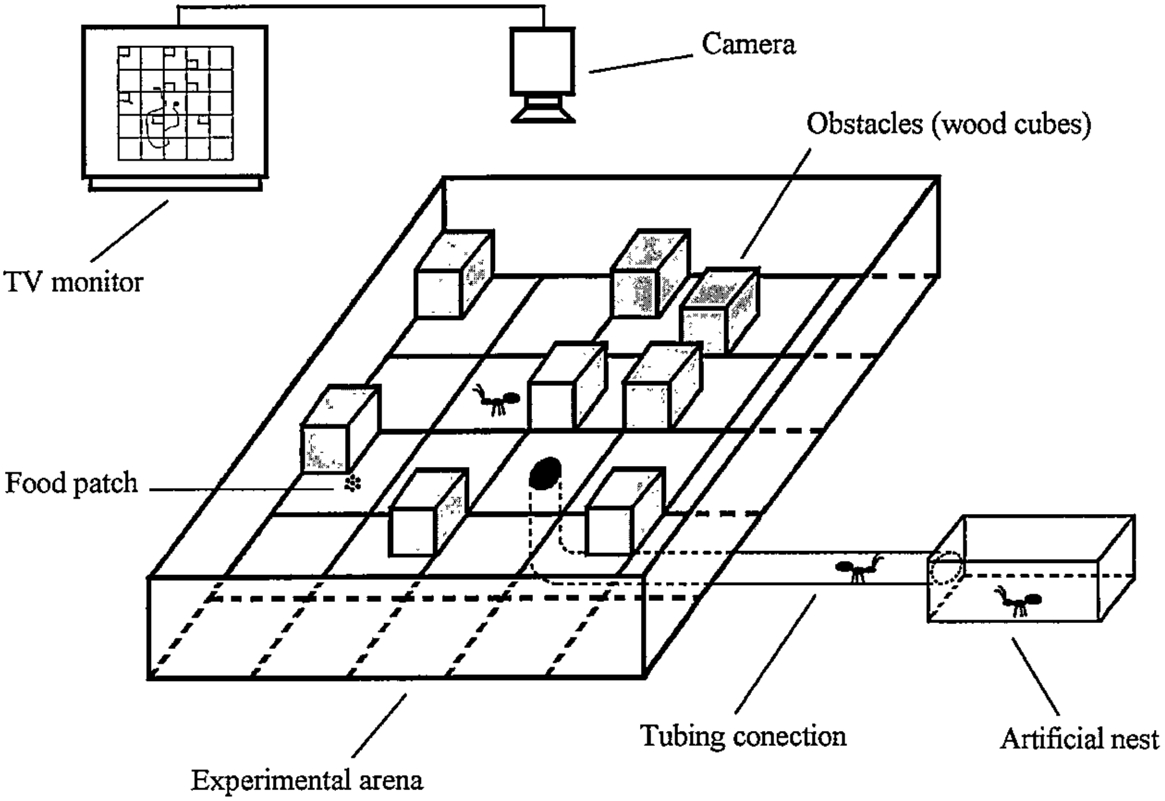
Camera
Obstacles (wood cubes)
TV monitor
Food patch
Tubing conection
Artificial nest
Experimental arena

Figure 2

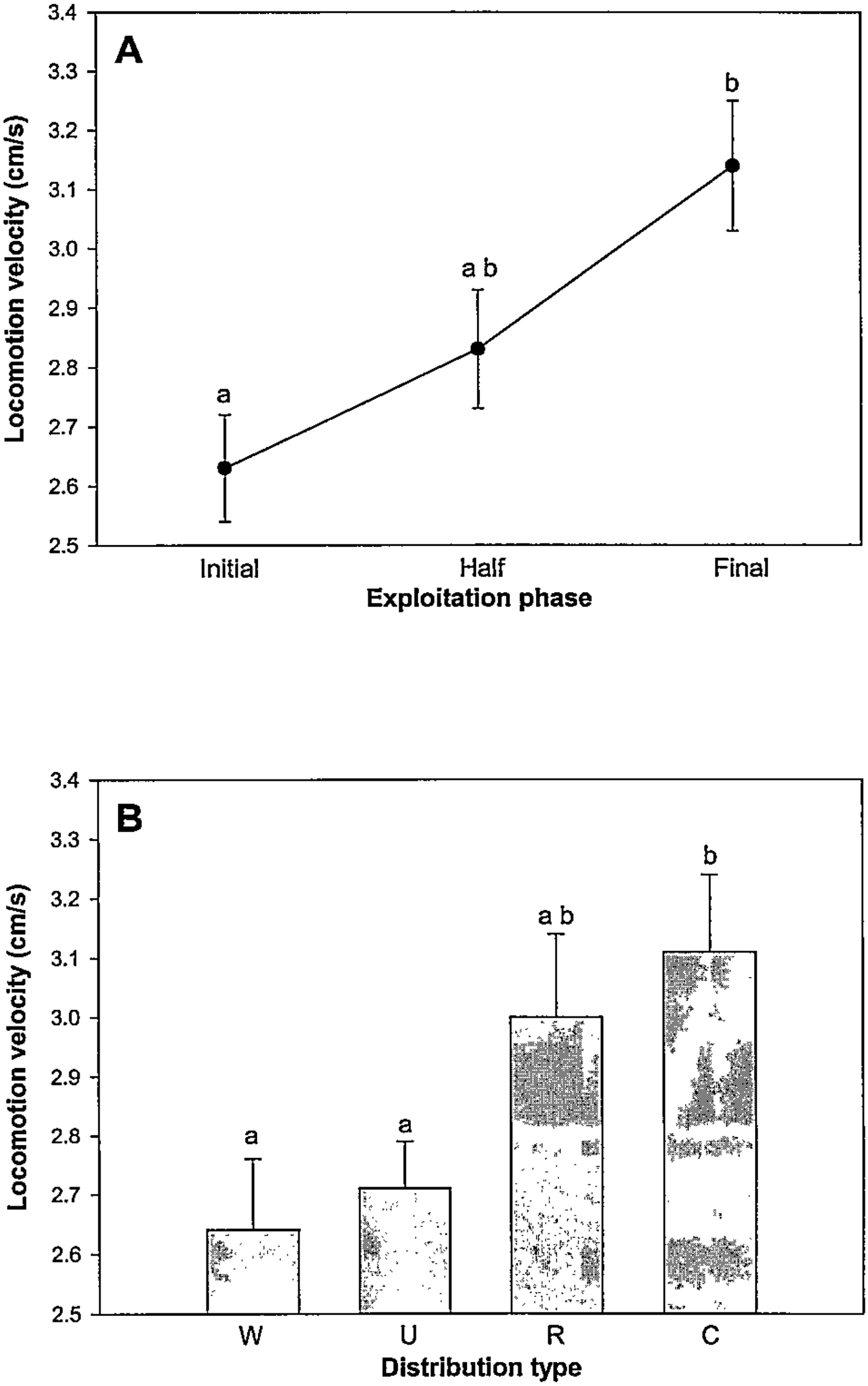
A
Locomotion velocity (cm/s)
3.4
3.3
3.2
3.1
3.0
2.9
2.8
2.7
2.6
2.5
a
a b
b
Initial
Half
Final
Exploitation phase
B
Locomotion velocity (cm/s)
3.4
3.3
3.2
3.1
3.0
2.9
2.8
2.7
2.6
2.5
a
a
a b
b
W
U
R
C
Distribution type

Figure 3

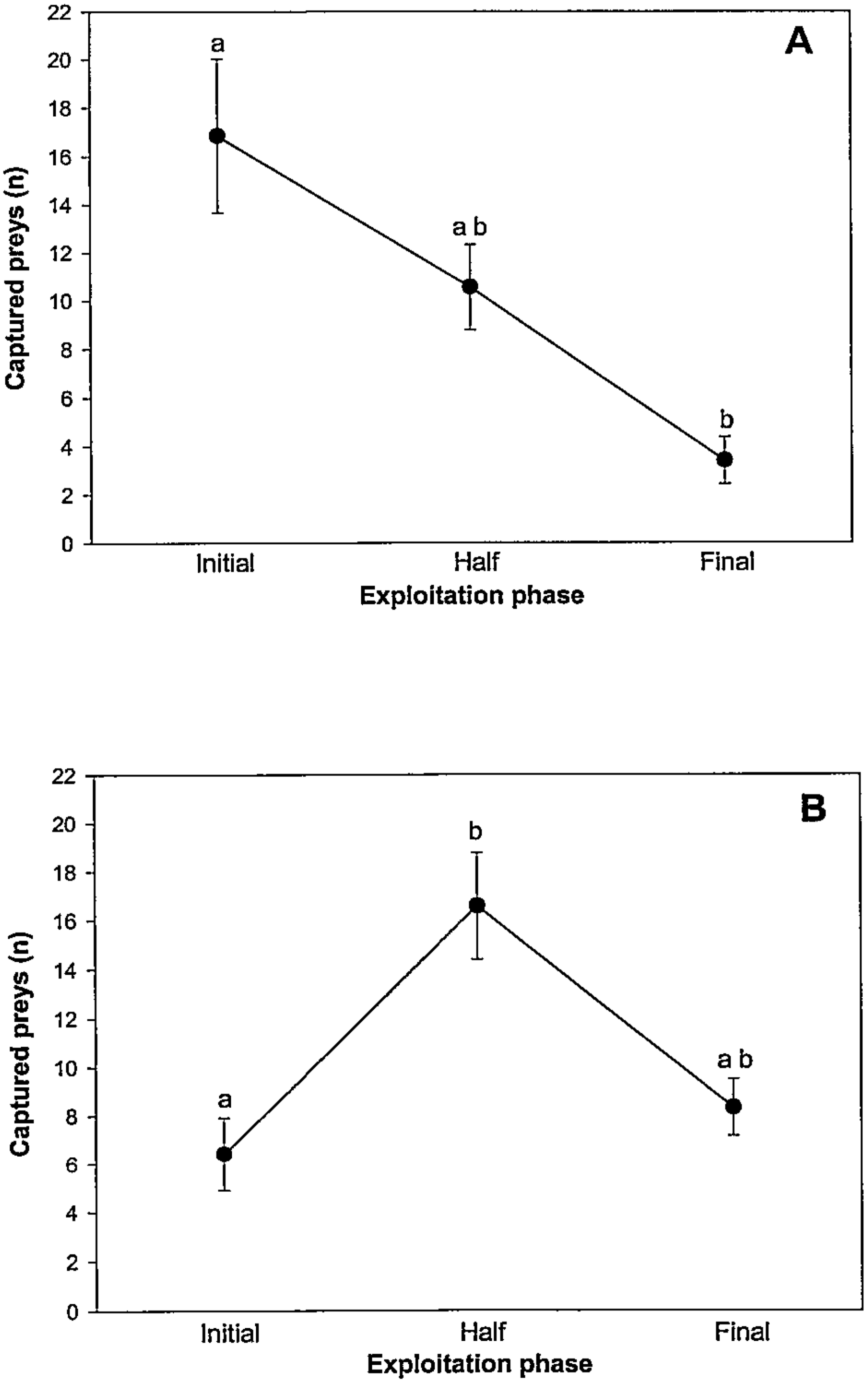
A
Captured preys (n)
22
20
18
16
14
12
10
8
6
4
2
0
a
a b
b
Initial
Half
Final
Exploitation phase
B
Captured preys (n)
22
20
18
16
14
12
10
8
6
4
2
0
b
a
a b
Initial
Half
Final
Exploitation phase

Figure 4

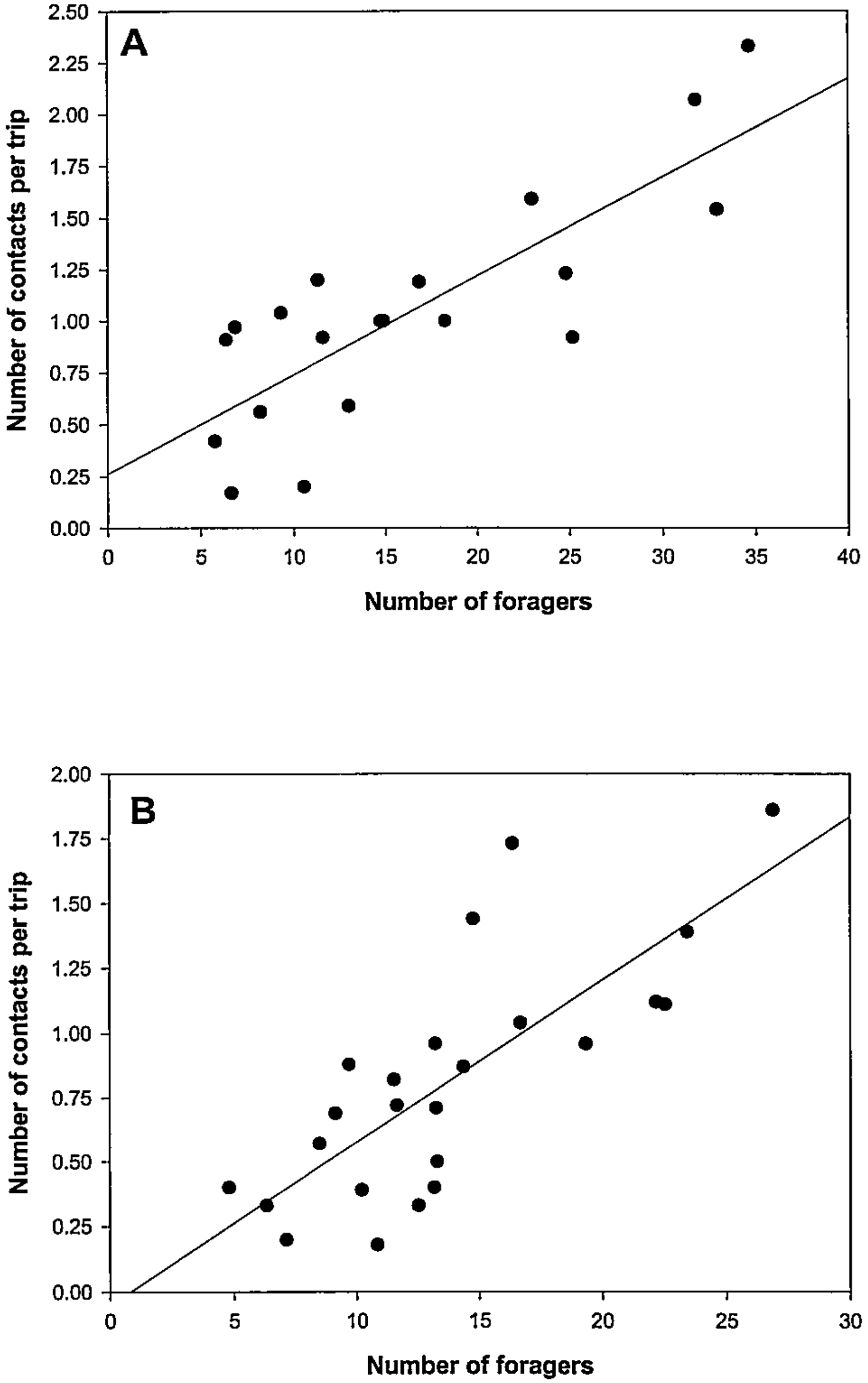
A
Number of contacts per trip
2.50
2.25
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
0
5
10
15
20
25
30
35
40
Number of foragers
B
Number of contacts per trip
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
0
5
10
15
20
25
30
Number of foragers

Figure 5

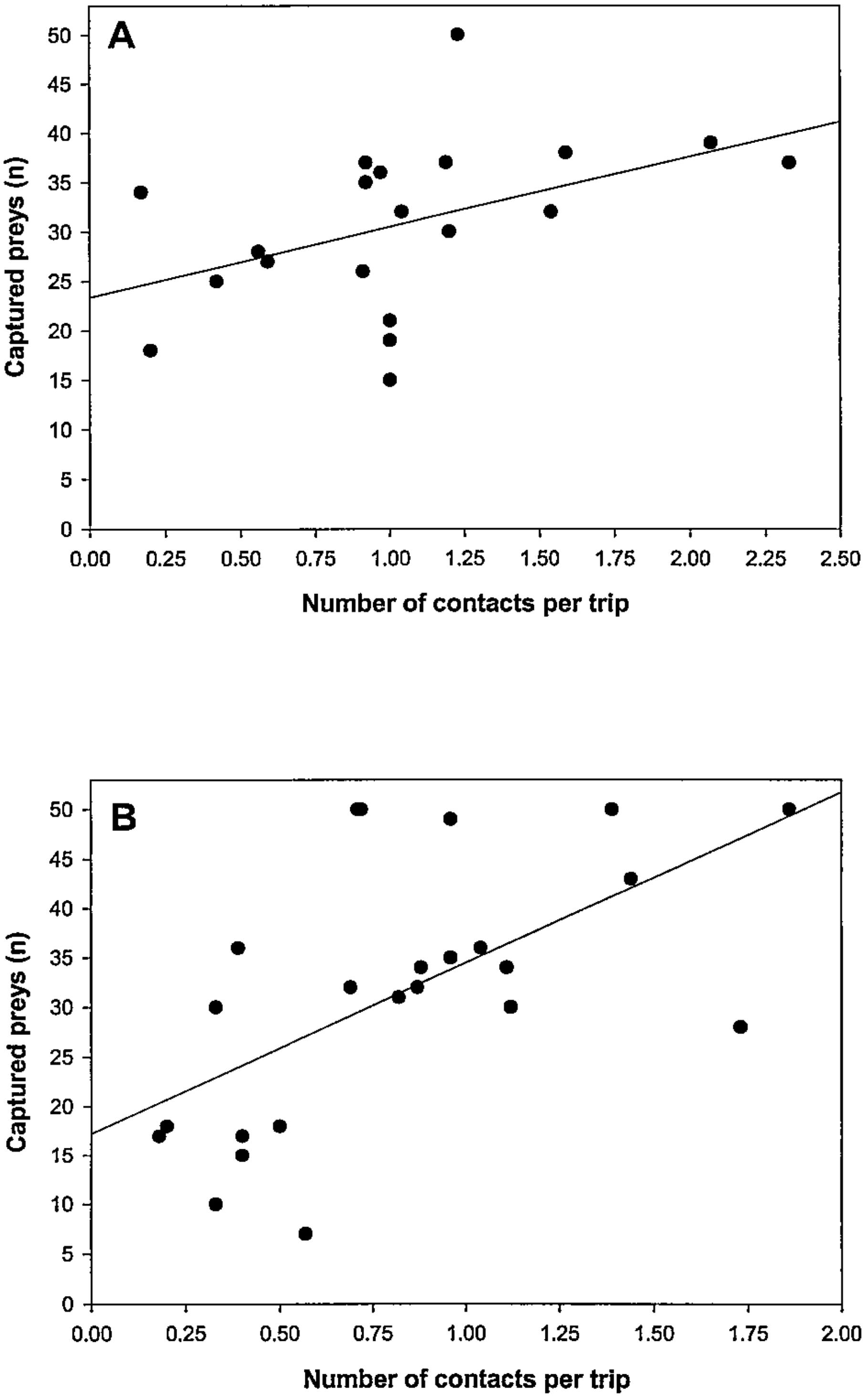
A
Captured preys (n)
0
5
10
15
20
25
30
35
40
45
50
0.00
0.25
0.50
0.75
1.00
1.25
1.50
1.75
2.00
2.25
2.50
Number of contacts per trip
B
Captured preys (n)
0
5
10
15
20
25
30
35
40
45
50
0.00
0.25
0.50
0.75
1.00
1.25
1.50
1.75
2.00
Number of contacts per trip

Figure 6

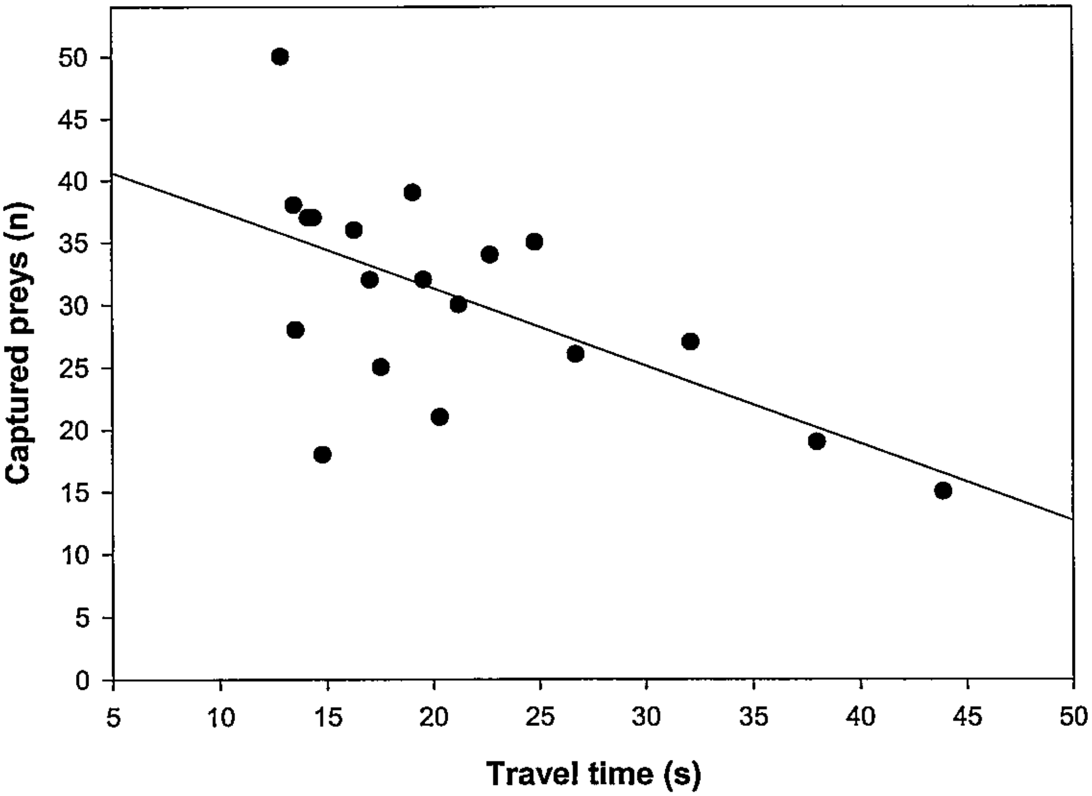
Captured preys (n)
0
5
10
15
20
25
30
35
40
45
50
5
10
15
20
25
30
35
40
45
50
Travel time (s)

Table 1. (A) MANOVA of exploitation time, spatial heterogeneity, ant species, and interaction effects on different dependent variables (number of foragers, path length, travel time, locomotion velocity, and captured prey). **(B)** Repetead measures ANOVAs for locomotion velocity and captured prey.

(A) Multivariate test of significance

Effect	Wilk's lambda	F	Numerator df	Denominator df	P
Time	0.731	3.530	10	208	0.0002
Heterogeneity	0.912	0.654	15	287	0.8285
Species	0.823	4.487	5	104	0.0009
T x H	0.834	0.646	30	418	0.9271
T x S	0.787	2.640	10	208	0.0047
H x S	0.841	1.239	15	287	0.2415
T x H x S	0.899	0.372	30	418	0.9991

(B) Univariate repetead measures tests

		Locomotion velocity			Captured prey		
Effect	df	MS	F	P	MS	F	P
Time	2	2.319	8.442	0.0004	700.234	8.133	0.0005
Heterogeneity	3	0.245	0.892	0.4478	55.812	0.648	0.5857
Species	1	4.684	17.049	0.0001	1.034	0.012	0.9129
T x H	6	0.315	1.146	0.3406	54.289	0.631	0.7055
T x S	2	0.053	0.192	0.8256	924.537	10.738	0.0001
H x S	3	0.981	3.569	0.0165	8.014	0.093	0.9637
T x H x S	6	0.094	0.344	0.9121	35.522	0.413	0.8693

Table 2. Results of a repeated-measured two-way ANOVA for the effects of exploitation time and spatial heterogeneity and their interaction on different dependent variables of the colonies *Camponotus morosus* (A) and *Camponotus chilensis* (B).

Source	df	SS	MS	F	P
(A) *Camponotus morosus*					
Locomotion velocity					
Time	2	1.712	0.856	3.448	0.083
Heterogeneity	3	1.110	0.370	0.843	0.496
Time x Heterogeneity	6	1.224	0.204	0.820	0.565
Error	24	5.976	0.249		
Captured prey					
Time	2	1811.434	905.717	8.353	<0.01
Heterogeneity	3	50.799	16.933	0.156	0.925
Time x Heterogeneity	6	212.298	35.383	0.326	0.920
Error	24	1240.872	51.703		
(B) *Camponotus chilensis*					
Locomotion velocity					
Time	2	3.166	1.583	9.578	<0.01
Heterogeneity	3	2.712	0.904	5.553	<0.05
Time x Heterogeneity	6	1.236	0.206	0.991	0.449
Error	30	6.240	0.208		
Captured prey					
Time	2	1400.778	700.389	4.487	<0.05
Heterogeneity	3	149.667	49.889	1.453	0.267
Time x Heterogeneity	6	337.998	56.333	1.206	0.330
Error	30	1401.660	46.722		

Table 3. (A) Summary of the procedure and **(B)** results of a forward-stepwise multiple linear regression model on the effect of movement path variables and antennal contacts on the number of captured prey by *Camponotus chilensis* colonies.

(A) Procedure

Step	Variable entered	F	Significance	r^2 ajusted	R^2 change
1	Head contacts	12.597	0.0019	0.364	0.364
2	Path length	2.781	0.1102	0.438	0.074

(B) Results

Variable	Slope	Significance
Head contacts	15.126	<0.01
Path length	-0.187	0.110
Constant	30.363	0.003

Regression Model Summary: $R^2 = 0.44$; $F_{2,21} = 8.19$; $p < 0.01$

Table 4. (A) Summary of the procedure and **(B)** results of a forward-stepwise multiple linear regression model on the effect of movement path variables and antennal contacts on the number of captured prey by *Camponotus morosus* colonies.

(A) Procedure

Step	Variable entered	F	Significance	r^2 ajusted	R^2 change
1	Travel time	11.367	0.0036	0.387	0.387
2	Head contacts	4.147	0.0576	0.507	0.120

(B) Results

Variable	Slope	Significance
Travel time	-0.555	<0.01
Head contacts	5.509	0.057
Constant	36.628	<0.001

Regression Model Summary: $R^2 = 0.51$; $F_{2,17} = 8.75$; $p < 0.01$

CAPÍTULO 5

Foraging at the distance in harvester ants (*Pogonomyrmex barbatus*): influence of habitat heterogeneity, information transfer, and locomotion performance

ABSTRACT

The distance between the nest and the food patch determines prey selection, energetic and time costs, and mortality risks experienced by ants during food searching and transportation. Besides, structural characteristics of the habitat, abiotic factors, and patchy distribution of resources restrict locomotion and foraging success of workers. Encounters among foragers allow information transfer about food quality and stimulate the recruitment of nesmates. I studied the influence of habitat heterogeneity, information transfer, and locomotion behavior on the foraging performance of the red harvester ant (*Pogonomyrmex barbatus*) colonies. In a locality of the Chichuahuan desert I selected 9 colonies of *P. barbatus*, and offered a novel food patch located at different distances from the nest entrance. Substratum heterogeneity was estimated as the proportion of ground surface covered by physical elements that restrict ant locomotion, and soil temperature around each colony was recorded. I video recorded the behavior of colonies and analyzed the following variables: number of prey captured by colony, the duration of patch exploitation, the number of active foragers, the number of head contacts per forager per trip, and invested time in inbound travels. I estimated locomotion velocities in the last 30 cm of return trips. In food patches located at the greatest distance, the colonies collected a lower number of preys, invested more time in patch exploitation, and exhibited a lower rate of resource removal. During the final phase of exploitation, colonies removed a greater number of preys. At distances near to the nest (1-4 m), trip duration decreased and running speed increased through time. A multiple regression analysis revealed that prey removal increased with greater number of foragers, shorter travel times, and low soil temperature. Aggressive encounters between foragers of neighbor colonies restrict collection of food at more distant patches from the nest. Colonies that used "trunk trails" during their foraging movements exploited the resources successfully. Possibly, use of chemical, visual and celestial signals increase locomotion performance of foragers. A shorter travel time would be a strategy that minimizes the energetic constrains of load transporting, diminishing the risk of predation and the loss of thermal balance, maximizing the consumption of resources per time unit. In this study I document a novel relationship between locomotion and foraging performance in harvester ant colonies throughout time.

Key words: *Pogonomyrmex barbatus*, food patch, substratum heterogeneity, soil temperature, antennal contacts, travel time, locomotion velocity

INTRODUCTION

Ants are central place foragers that transport one load of food at a time. Food retrieval is determined by biotic (e.g., resources, competitors, intrinsic characteristics of the colony) and abiotic (e.g., temperature, rain, physical barriers of the substratum) factors. These multiple aspects have precluded tests of predictions from central place foraging theory. For example, some studies support that a greater distance between the nest and food patches increases selection of prey with larger size and/or richer energy content (e.g., Schmid-Hempel 1984; Bailey and Polis 1987; Crist and MacMahon 1992; Roces and Nuñez 1993). However, others works have failed to find any relationship and emphasize time and energy costs of individuals during exploration trips, searching and food transportation (e.g., Lighton et al. 1987; Fewell 1988; Fewell et al. 1996; Morehead and Feener 1998).

A factor that affects foraging behavior of ants is mortality risk (e.g., Nonacs 1990). Greater path lengths and/or longer time invested in foraging trips increases the loss of thermal balance (e.g., Lighton and Bartholomew 1988) and the risk of predation and parasitism (e.g., Feener and Moss 1990). Habitats associated to distant resource patches represent dangerous areas that could trigger a low recruitment (e.g., Nonacs and Dill 1988, 1990). On the other hand, structural characteristics of the substratum (e.g., vegetation cover), abiotic factors (e.g., soil temperature), and a patchy distribution of resources (e.g., seeds) restrict the movement and foraging success of ants (Crist and MacMahon 1991a; Crist and Haefner 1994; Crist and Weins 1994). In this respect, it has been suggested that locomotion performance would have an effect on resource removal rate in ants (e.g., Fewell 1988), but to the best of my knowledge, no previous study has examined this relationship. Besides, the encounter rate between workers that carry out different tasks (e.g., trail patrollers, foragers with food, foragers within food) allows information transfer about quality of novel resources and can stimulate the recruitment of nestmates (e.g., Adler and Gordon 1992; Gordon 2002). In particular, brief antennal contacts between two ants allow decision making about feeding activities, through physiological and chemical mechanisms of recognition (e.g., Wagner et al. 1998, 2000, 2001).

Harvester ants are specially common in arid and semiarid zones (Hölldobler and Wilson 1990; MacMahon et al. 2000; Johnson 2001). The genus *Pogonomyrmex* constitutes one major group of granivourous ants in the deserts of North America (Davidson 1977a,b; Taber 1998; MacMahon et al. 2000; Johnson 2000, 2001). These ants collect seeds from a range of annual plants, but they show preferences for only a few species based on size and energy content criteria (Davidson 1977a; Whitford 1978; Crist and MacMahon 1992; Gordon 1993; Morehead and Feener 1998). Species that show greater efficiency in the exploitation of resources are those that use "trunk trails", which are permanent cleared tracks leading from the nest to the foraging area (Hölldobler 1976; Harrison and Gentry 1981; Gordon 1991; Crist and MacMahon 1991a; Mull and MacMahon 1997). The daily and/or seasonal foraging territories are not rigid but a flexible character of these colonies (Gordon 1991, 1999). In this way, the establishment of "trunk trails" and the foraging performance of a colony depend on factors like seed availability (Fewell 1990; Crist and MacMahon 1991a; Gordon 1991, 1993), vegetation cover (Hölldobler 1976; Fewell 1988; Gordon 1993; Crist and Wiens 1994), interaction with neighbouring colonies (Gordon 1992, 1995; Gordon and Kulig 1996; Brown and Gordon 2000), action of predators (Whitford and Bryant 1979; Rissing 1981; MacKay 1984; MacMahon et al. 2000), and encounter rates and chemical recognition between workers that carry out tasks outside the nest (Gordon 1984, 1986; Gordon and Mehdiabadi 1999; Greene and Gordon 2003).

The aim of this study was to evaluate the influence of habitat heterogeneity (soil temperature, vegetation cover), information transfer (forager abundance, antennal contacts), and locomotion performance (travel time, locomotion velocity) on the foraging performance of harvester ant colonies confronted to a novel food patch located at different distances from the nest entrance. Specifically, I asked the following questions. (1) How does the spatial heterogeneity of the substratum affect resource removal? (2) What improvements produce the exchange of information between individuals on feeding activities? (3) Is there a causal relationship between locomotion and foraging performance? I predicted that: (i) landscapes with more physical constrains reduce foraging performance, (ii) greater number of workers and antennations between nestmates increases foraging success, and, (iii) shorter travel times and higher running speeds increase prey capture.

MATERIALS AND METHODS

Study site and species

I conducted this study in the Chichuahuan desert, approximately 3 km north of Portal, Arizona, USA. The 3 ha site is on an alluvial fan, and the vegetation varies from bare ground with small bunches of grass to primarily shrubs such as *Acacia constricta*, *Prosopis glandulosa*, *Gutierrezia sarothrae*, and *Ephedra* spp.

The species studied was the red harvester ant (*Pogonomyrmex barbatus*). The workers of this species have a body weight mean of 14.0 mg (Morehead & Feener 1998). Colonies of *P. barbatus* partition spatially and temporally the foraging task among their workers. Trail patrollers emerge each morning before foragers. These patrollers eventually converge on a few foraging directions to be used each day. The last patrollers return when foragers begin to emerge (Gordon 1986, 1991). Foragers use those directions previously used by the patrollers (Gordon 1991) and will ignore food sources not visited earlier by patrollers (Gordon 1983). Later, the returning of successful foragers determine the rate at which inactive ants leave the nest to forage (Gordon 1991, 2002). Colonies sometimes establish and use “trunk trails” (Hölldobler 1976), as well as other habitual trails, across bare soil, which are not apparent when not in use by foragers (Gordon 1991). A mature colony of *P. barbatus* has a set of about 8 habitual foraging directions, but only 3-5 of these are used each day (Gordon 1991). Most foragers (> 90%) stay out until they find a food item (Gordon 1991), and a worker can spend up to an hour searching, although the average foraging trip is about 20 minutes (Gordon and Kulig 1996). The foraging behavior of *P. barbatus* indicates that there is intraspecific competition for foraging behavior (e.g., Gordon 1991). Therefore, foragers from old colonies avoid conflict with neighbours over the boundaries of a given colony foraging area (Gordon 1987, 1989, 1991, 1992).

Experimental design

The fieldwork was carried out in August 2002 during the summer season. In the field, *P. barbatus* transport natural loads with a range between 0.05 – 5.20 mg (Morehead and Feener 1998). I used compacted sugar microspheres (7.21 ± 0.07 mg, mean ± SE, n= 200) comercially available as experimental prey. Although the size of experimental food items was in the upper range of the natural prey distribution of this species, this size was needed to assure that (i) prey items were detectable from video recordings, and (ii) prey variability was low or nil. Further, my observations revealed that prey handling was not affected by these food items. I selected 9 old colonies of *P. barbatus* (see Fig. 1) to which I offered a food patch of 200 microspheres. For each colony, and in different days selected at random, I placed the food patch at five different distances from the nest entrance: 1, 2, 4, 8 and 16 m. These distances were within the normal foraging range of this species (see Hölldobler 1976; Gordon 1995). Every day I checked at 5:30 AM the activity of three colonies, and observed during 30 minutes the foraging routes chosen by trail patrollers. Later, I offered the food patch in the direction of the main route. Resource patches were set approximately at 6:00 AM and I video recorded (Sony camera, model CCD-TRV 108) the movement and feeding behavior of forager workers until the resource was depleted and/or the activity stopped. The camera focused over a spatial window of 35 x 30 cm (length x width), within which I observed both the nest opening and an area within 30 cm from the foraging trail (I placed a 30 cm graduated ruler in the top edge of the image). Videos were watched and the following variables were measured: number of captured prey per colony, duration of patch exploitation, number of active foragers, number of head contacts per forager per trip, time of inbound travels, and I estimated locomotion velocity in the last 30 cm of return trips.

In the field, I measured environmental temperature around each colony at two millimeters above the soil with a digital thermometer (Checktemp, precision ± 0.1 °C). Landscape spatial heterogeneity was estimated with linear transects that were arranged through the matrix that separated the entrance of the nest and the food patch. Following Johnson et al. (1992), I calculated a heterogeneity index that considers the proportion of ground surface covered by physical elements that could inhibit ant locomotion (e.g., stones, twigs, leaves, and/or grass; 1 cm width and length, or larger), in relation to the total surface that include bare ground. For example, if 10 cm are covered by stones and 20 cm by grass, out of a total distance of 100 cm, then the heterogeneity index has a value of 0.3. I found that ants confront higher spatial heterogeneities when distance to the food patch is greater ($r^2 = 0.58$, $t = 7.76$, $p \ll 0.0001$; Fig. 2).

I continuously counted the number of foragers that go across (in the way to the food patch) a point located at 20 cm from the nest entrance in foraging trail. A high density of individuals has been correlated with an increase in antennal contact rates per ant (e.g., Gordon 1996), and with decision making through chemical mechanisms of recognition (e.g., Greene and Gordon 2003). In this way, I quantified the number of brief head to head contacts that each successful forager experienced in their inbound trips. These contacts were used as an estimate of information transfer. I followed the methodology and criterion used by Gordon et al. (1993) and Burd and Aranwela (2003) to determine an effective contact between two ants.

Finally, I quantified minute by minute, the number of sugar microspheres captured by the colony, and considered a successful removal when a prey was introduced to the nest by a worker. The duration of patch exploitation was estimated as the time taken by a colony to remove 100% of resources or until activity stopped. For analysis, the exploitation time was divided in three phases (initial, half, final) with the objetive of evaluating changes in the feeding performance through time. The foraging performance at the colony level was evaluated by means of total resource removal rate (i.e., number of captured prey / minutes invested in patch exploitation).

Statistical analysis

A one-way ANOVA was carried out to evaluate the effect of food patch distance on the number of captured prey, time duration of patch exploitation, and resource removal rate. Similarly, the influence of exploitation phase on different dependent variables, was also analyzed with a one-way ANOVA, with soil temperature used as covariate. The effect of foragers, contacts, travel time, locomotion velocity, soil temperature and spatial heterogeneity on total resource removal rate was analyzed with a multiple linear regression. Given the nature of the data, the effect of different variables on resource removal carried out by ant colonies was analyzed for two categories of distances (between 1-4 m, and 8-16 m). In these tests the colony was used as the sample unit, and hence data correspond to the mean of foragers per colony. All tests were carried out with Statistica 6.0 software (StatSoft Inc.). Data shown correspond to the mean ± one standard error, and the significance of the statistical tests was fixed to $\alpha = 0.05$. Data satisfied the assumptions of each test.

RESULTS

Patch distance

The number of captured prey by colony was significantly lower when the food patch was located at a greater distance from the nest entrance ($F_{4,40} = 9.65$, $p < 0.0001$; see Fig. 3a). At distances of 1 m the colonies captured 200.00 ± 0.00 microspheres of sugar (mean ± SE, n= 9 colonies), 199.89 ± 0.11 microspheres (range: 199-200) when the resource was 2 m distant, 199.44 ± 0.55 (range: 195-200) when it was at 4 m, 195.78 ± 4.22 (range: 162-200) at 8 m, and 88.89 ± 35.14 (range: 0-200) at 16 m. The time invested in patch exploitation was significantly higher when the resource patch was more distant from the nest ($F_{4,40} = 13.46$, $p << 0.0001$; see Fig. 3b). At distances of 1 m the colonies invested 32.44 ± 3.50 minutes (range: 13-45), 36.44 ± 4.41 minutes (range:

18-59) when the food was at 2 m, 40.11 ± 7.16 (range: 23-88) when it was at 4 m, 60.89 ± 13.67 (range: 32-161) at 8 m, and 104.22 ± 7.61 (range 60-120) at 16 m. Resource removal rate was significantly lower when the food patch was more distant from the nest open ($F_{4,40} = 8.82$, $p < 0.0001$; see Fig. 3c). At distances of 1 m the colonies removed 7.12 ± 1.17 food items per minute (range: 4.44-15.38), 6.26 ± 0.85 preys per minute (range: 3.38-11.11) at 2 m, 5.99 ± 0.76 (range: 2.27-8.69) at 4 m, 4.17 ± 0.59 (range: 1.01-6.25) at 8 m, and 1.11 ± 0.46 (range: 0.00-3.33).

Exploitation phase

A general analysis (for food patches distant at 1-16 m) showed that the number of captured prey was affected only by exploitation phase ($F_{2,80} = 51.68$, $p << 0.0001$), with more food retrieved through time. For resource patches located between 1-4 m from nest entrance, the number of captured prey was significantly affected by exploitation time ($F_{2,50} = 27.89$, $p << 0.0001$; Fig. 4a). The number of food items removed during the final phase (85.39 ± 6.80, mean ± SE) and the half phase (85.94 ± 6.32) was 3.1 times greater than during the initial phase (27.83 ± 3.73). Similarly, for resource patches located between 8-16 m from nest open, the number of captured prey was also significantly affected by exploitation phase ($F_{2,26} = 41.46$, $p << 0.0001$; Fig. 4b). During the final phase, the number of food items removed (76.87 ± 15.66, mean ± SE) was 1.8 times greater than during the half phase (43.73 ± 9.69), and 6.0 times greater than during the initial phase (12.73 ± 2.81).

In food patches located at 1-4 m, the travel time of inbound foragers was significantly affected by exploitation time ($F_{2,50} = 5.95$, $p < 0.01$; Fig. 5a). During the final phase of experimentation, trip time (10.90 ± 0.72 s, mean ± SE) was 11% lower than during half phase (12.31 ± 0.74), and 25% lower than during the initial phase (14.45 ± 0.74). The locomotion velocity also was significantly affected by exploitation time ($F_{2,50} = 7.91$, $p < 0.01$; Fig. 5b). During the final phase of experimentation, running speed (3.15 ± 0.17 cm/s, mean ± SE) was 12% greater than during half phase (2.76 ±

0.14), and 26% greater than during the initial phase (2.34 ± 0.12). However, for resource patches located at 8-16 m, I did not find an effect of exploitation time on the locomotion performance of successful foragers returning to nest. Besides, for both sets of distances I did not find effect of time on the number of active foragers and head contacts per capita.

Foraging performance

Considering resource patches located at 1-16 m, a multiple linear regression with forward-stepwise procedure (Table 1A) shown that the travel time, soil temperature and number of foragers have a significant effect on the resource removal rate, and that these variables explained a significant fraction (56%) of the variation in foraging performance of colonies (Table 1B). Considering the sign of the estimated parameters (slope), I suggest that a greater number of foragers and shorter travel time and soil temperature increase prey removal.

The same analysis (Table 2A) was carried out for food patches located between 1-4 m from nest entrance, and revealed that the number of foragers, soil temperature and locomotion velocity have a significant effect on the food retrieval, explaining a 78% of the variation in foraging performance of the colonies (Table 2B). A greater number of foragers and locomotion velocities increase prey removal, however, a higher soil temperature diminishes removal rate.

For food sources located at 8-16 m from nest open, the analysis (Table 3A) detected that the travel time and locomotion velocity have a significant effect on the foraging performance, and that both variables described a 62% of the variation in removed resources by the colonies (Table 3B). A lower travel time and locomotion velocities increase prey removal rate.

DISCUSSION

When food sources were located at greater distance from the nest entrance, colonies of *P. barbatus* collected a lower number of prey, invested more time in patch exploitation, and obtained a lower resource removal rate. These results agree with a greater activity of foraging and seed removal of *Pogonomyrmex* sp. in sites near the nest (e.g., between 4-8 m for *P. occidentalis*; Crist and MacMahon 1991a,b, 1992; Crist and Wiens 1994). Therefore, a food patch at 16 m represents a trade off in the foraging decision for a colony. The allocation of workers to exploit a novel but distant food patch implies benefits in energetic and nutritious terms, but also time costs as animals experience higher predation risks, competitive interactions, and/or risk of hypertermia. For example, aggressive encounters reduce food capture because foragers who have fought remain a long time in the nest before initiating a new foraging trip (e.g., approximately 58 min in *P. californicus*; see De Vita 1979). In the case of *P. barbatus*, foraging territories overlap between neighboring colonies (e.g., Gordon 1991). Thus, ants from colonies of five years old or older, avoid encounters with ants from others colonies in boundary zones and reallocate their efforts to areas where contact is probably low or nil (e.g., Gordon 1992).

In my experiments, 5 out of 9 colonies did not discover the more distant resource patches, which were exploited by neighboring colonies. In different occasions, the colonies #547 and #734 exploited resources offered to the colony #429; colonies #148 and #215 monopolized the food offered to the colony #582; colonies #741 and #923 used the preys offered to the colony #547; and the colonies #992 and #236 exploited the patch offered to the colony #541 (see Fig. 1). In the case of the colony #540 the patch was exploited by the species *Dorymyrmex bicolor* whose nest was closer to the foraging routes. These "unsuccessful" colonies did not use "trunk trails" and their maximum displacements reached 9-12 meters. Possibly, these colonies experience a greater substratum spatial heterogeneity (see Fig. 2). Greater habitat heterogeneity restricts the probability of finding food and decreases information transfer between nestmates (e.g., Crist and Haefner 1994; Crist and Wiens 1994; Haefner and Crist 1994). Besides, the returning rate of successful foragers determines the levels of recruitment and the direction of main daily routes (e.g., Gordon 1991; Roces and Nuñez 1993). Thus, the workers that followed some of the tracks selected by patrollers can shift towards other directions when not reaching a threshold value of prey retrieved by invested time unit (e.g., Gordon 2002).

Although, in some of the successful colonies at distances of 16 m (e.g. colonies #486, #712) we observed aggressive encounters with the species *Aphaenogaster cockerelli* and *Solenopsis xyloni* during the beginning of patch exploitation, these confrontations did not affect the total removal of resources. The exploitation of a food patch by harvester ants would be an all-or-none decision, since those colonies that discovered the patch, removed the totality of prey. Besides, these successful colonies used "trunk trails" in their displacements of foraging, corroborating previous studies asserting the efficacy of these routes for exploiting resources (e.g., Hölldobler 1976; Fewell 1988, 1990; Crist and MacMahon 1991a). In these paths with no vegetation, ants move at greater speed and they obtain more energetic gains (e.g., Fewell 1988). The use of trail pheromones allows foragers to mark these paths with chemical signals, and thus to orient efficiently their outbound and inbound trips (e.g., Hölldobler et al. 2001). “Trunk trails” allows the avoidance of aggressive encounters with ants from neighbouring colonies (e.g., Hölldobler 1974, 1976), decrease the risk of predation (e.g., Fewell 1988), and they may represent a strategy for exploiting patchy distributed resources (seeds) in high density conditions (Davidson 1977b).

In the case of food patches located at different distances from the nest, an increase of captured prey through time can be linked to events of acquisition and use of information. For example, other species of ants use visual (e.g., walking beside of familiar landmarks, turning to the left or right of an obstacle) and celestial signals (e.g., orientation by using the azimuth of the sun, and the pattern of polarized light) that allow to guide their displacements (Collet et al. 1992; Wehner 1997; Akesson and Wehner 2002; Graham and Collet 2002). Besides, the use of chemical signals (e.g., recognition of cuticle hydrocarbons) allow ants to identify the tasks carried out by workers with which they have established contacts, and hence it may improve the foraging performance (e.g., Wagner et al. 1998, 2000, 2001).

My experiments with resource patches located at shorter distances from the nest (i.e., between 1-4 m) show that travel time diminishes and locomotion velocity increases through time, which could have implications on the success of resource exploitation. These findings are crucial since traditionally, locomotion and foraging behavior have been studied as independent events in the literature. Landscape ecology have studied the effect of spatial heterogeneity on the complexity of movement paths (e.g., With 1994; Wiens et al. 1995), but have not specified the stimulus that trigger movements, the changes that individual trajectories experience through time as a result of information accumulation, and the influence that locomotion performance can have on other behaviors. On the other hand, optimal foraging studies have not considered explicitly the movement complexity displayed by the organisms in the matrix between food patches (see e.g., Charnov 1976; Orians and Pearson 1979; Pyke 1984), and, therefore, they have not analyzed the consequences of habitat heterogeneity on feeding performance. In this work, I document a relationship between locomotion and foraging performance of harvester ant colonies, and how this relationship change throughout time.

It is possible to suggest that the relationship between locomotion and foraging is not expressed throughout time in food patches at 8-16 m from the nest, due to effects of dilution in the information transfer (e.g., lower number of contacts, "evaporation" of the chemical signals), energetic constrains in the transport of loads (e.g., Lighton et al. 1993), and/or physical barriers of the landscape that restrict the displacements (e.g., Wiens et al. 1995).

The multivariate analysis showed that for food patches located between 1-4 m from the nest entrance, a greater number of foragers have a positive effect on the resource removal rate. This corroborates that a collective work makes the performance of a task more effective (e.g., Detrain et al. 1990; Devigne and Detrain 2002). That is, individual behaviors apparently disordered are integrated in organized activities at the level of the colony. Besides, greater locomotion velocities allow efficient capture of prey (e.g., Fewell 1988), diminishes mortality risks (e.g., Fewell 1990), and minimize the energetic cost of load transportion (e.g., Morehead and Feener 1998). It is well documented that soil temperature has a important effect on the running speed and foraging behavior of harvester ants (Rissing 1982; Lighton et al. 1987; Weier and Feener 1995; Morehead and Feener 1998), due to problems associated at loss of thermal balance (Lighton and Bartholomew 1988).

In the case of food patches located at 8-16 m from the nest, a lower travel time would be a strategy that maximizes resource removal by time unit (e.g., Weier and Feener 1995). The contra-intuitive relationship between locomotion velocity and foraging performance can be the result of an increase in the time invested when individuals transport a standard weight of load but during a long time and at large distances (e.g., Weier and Feener 1995; Morehead and Feener 1998).

On a temporal scale of a pair of hours, resource removal rate in colonies of *P. barbatus* is determined by patch distance, soil temperature, the use of "trunk trails", presence of neighboring colonies, number of active workers, and the locomotion performance of foragers. This corroborates that in social insects the feeding behavior is a complex process that is influenced by multiple factors. Essentially, I emphasized the sensitivity that allows a harvester ants colony to adjust its foraging according to food availability and/or environmental conditions (Gordon 2002).

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LEGEND OF FIGURES

Figure 1: Spatial distribution of the *P. barbatus* colonies studied during summer 2002 (bold numbers), and their position respect to neighbouring nests. Each cell of the grid represent a distance ca. 33 m.

Figure 2: The relationship between spatial heterogeneity and distance to the food patch from nest entrance.

Figure 3: The effect of food patch distance on **(a)** the number of captured prey, **(b)** duration of patch exploitation, and **(c)** resource removal rate carried out by *P. barbatus* colonies. Values are mean ± SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See text for details.

Figure 4: The effect of exploitation phase on the number of captured prey by *P. barbatus* colonies for **(a)** food patches located between 1-4 m from nest entrance, and **(b)** resource sources located between 8-16 m from nest open. Values are mean ± SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See text for details.

Figure 5: The effect of exploitation phase on **(a)** travel time, and **(b)** locomotion velocity of *P. barbatus* successful foragers returning from food patches located between 1-4 m from nest entrance. Values are mean ± SE. Different letters above bars indicate significant differences (Tukey test *a posteriori*, $p < 0.05$). See text for details.

Figure 1

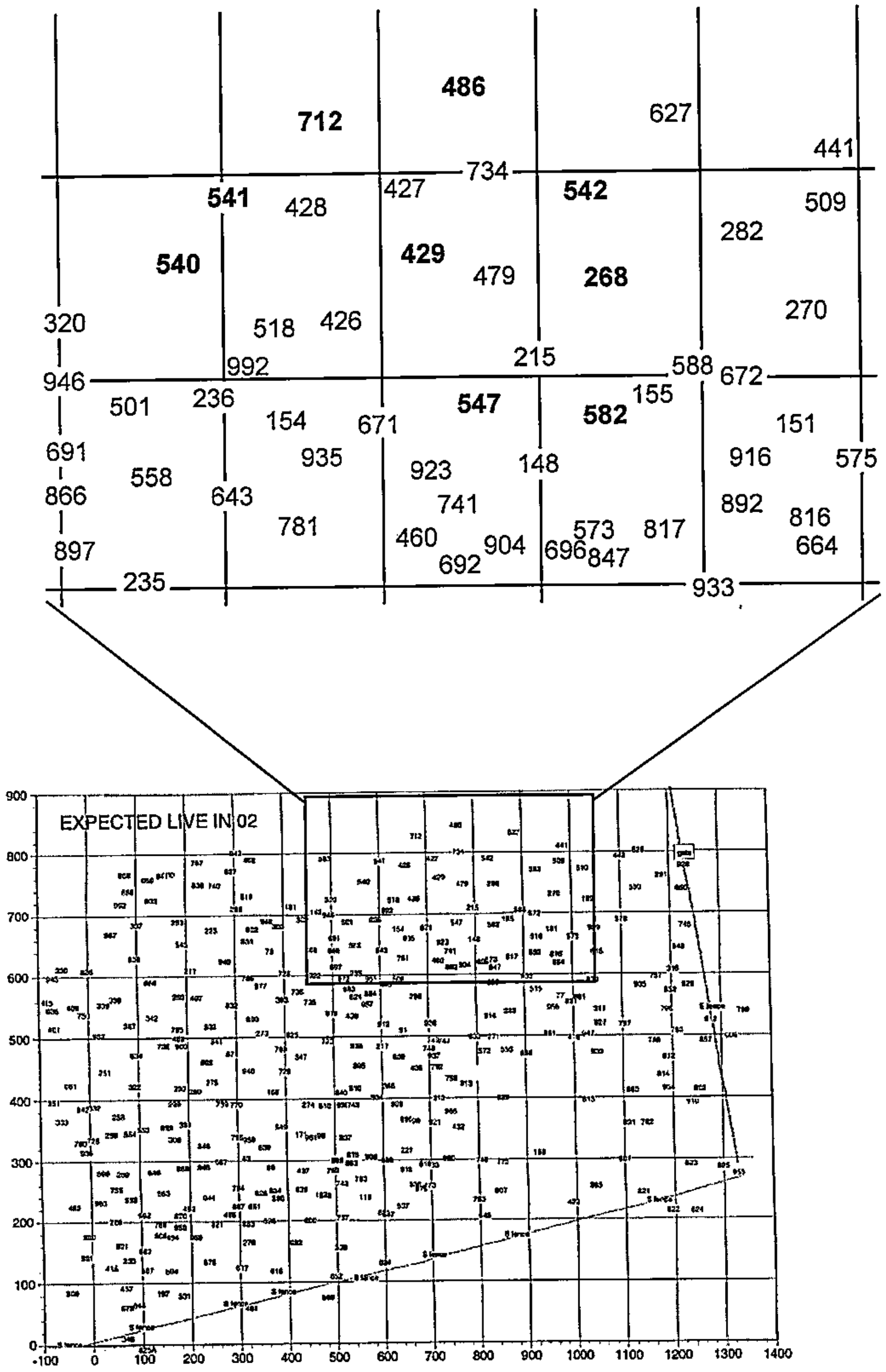
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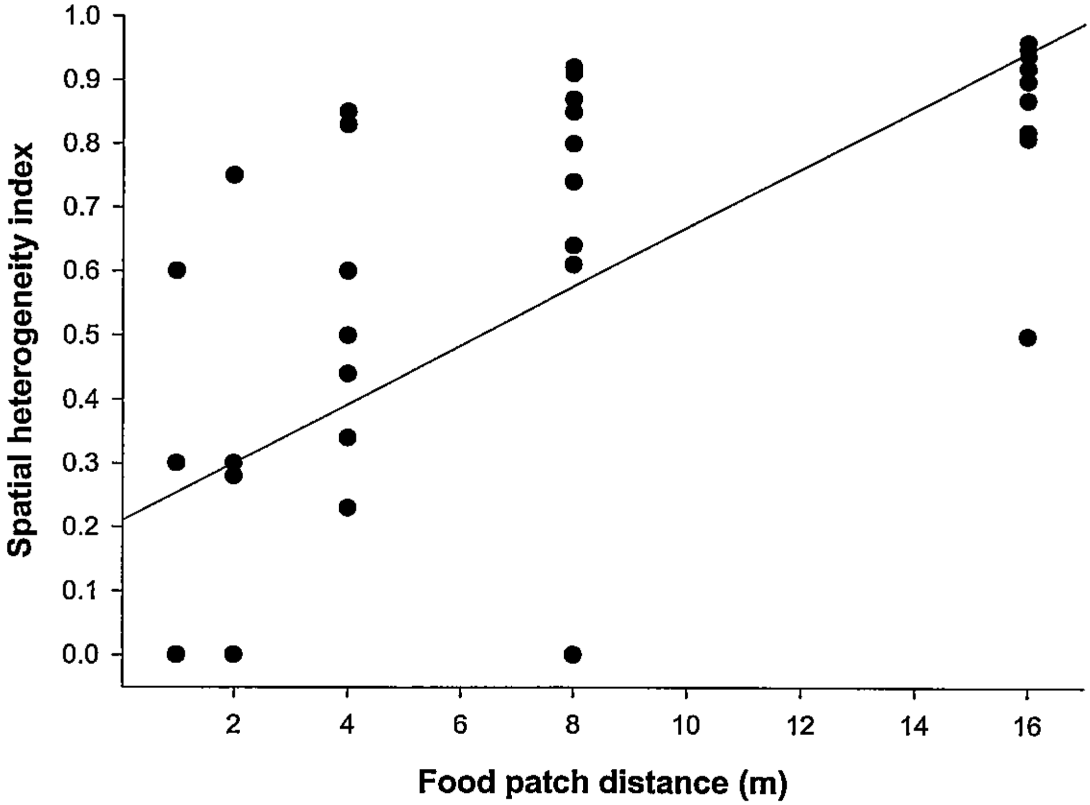
Figure 2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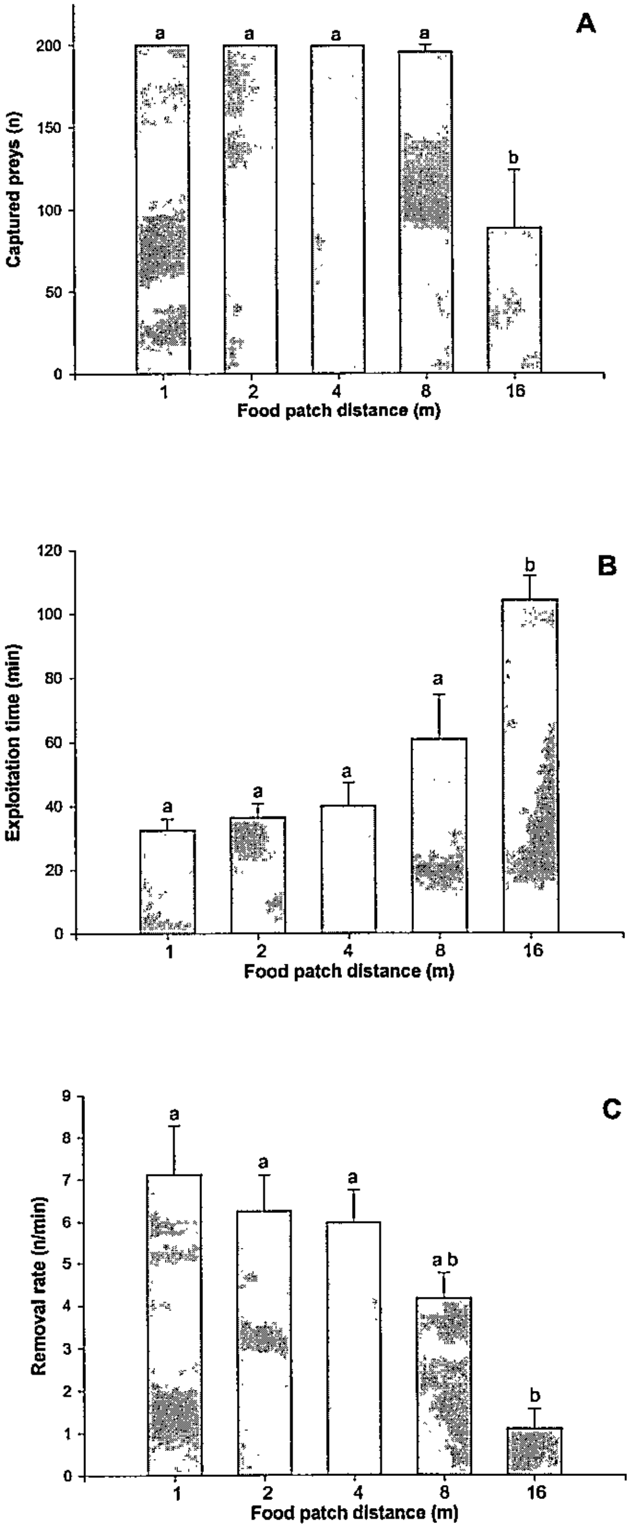
Food patch distance (m)

Figure 3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200
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b
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Food patch distance (m)
B
Exploitation time (min)
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40
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80
100
120
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a
b
1
2
4
8
16
Food patch distance (m)
C
Removal rate (n/min)
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16
Food patch distance (m)

Figure 4

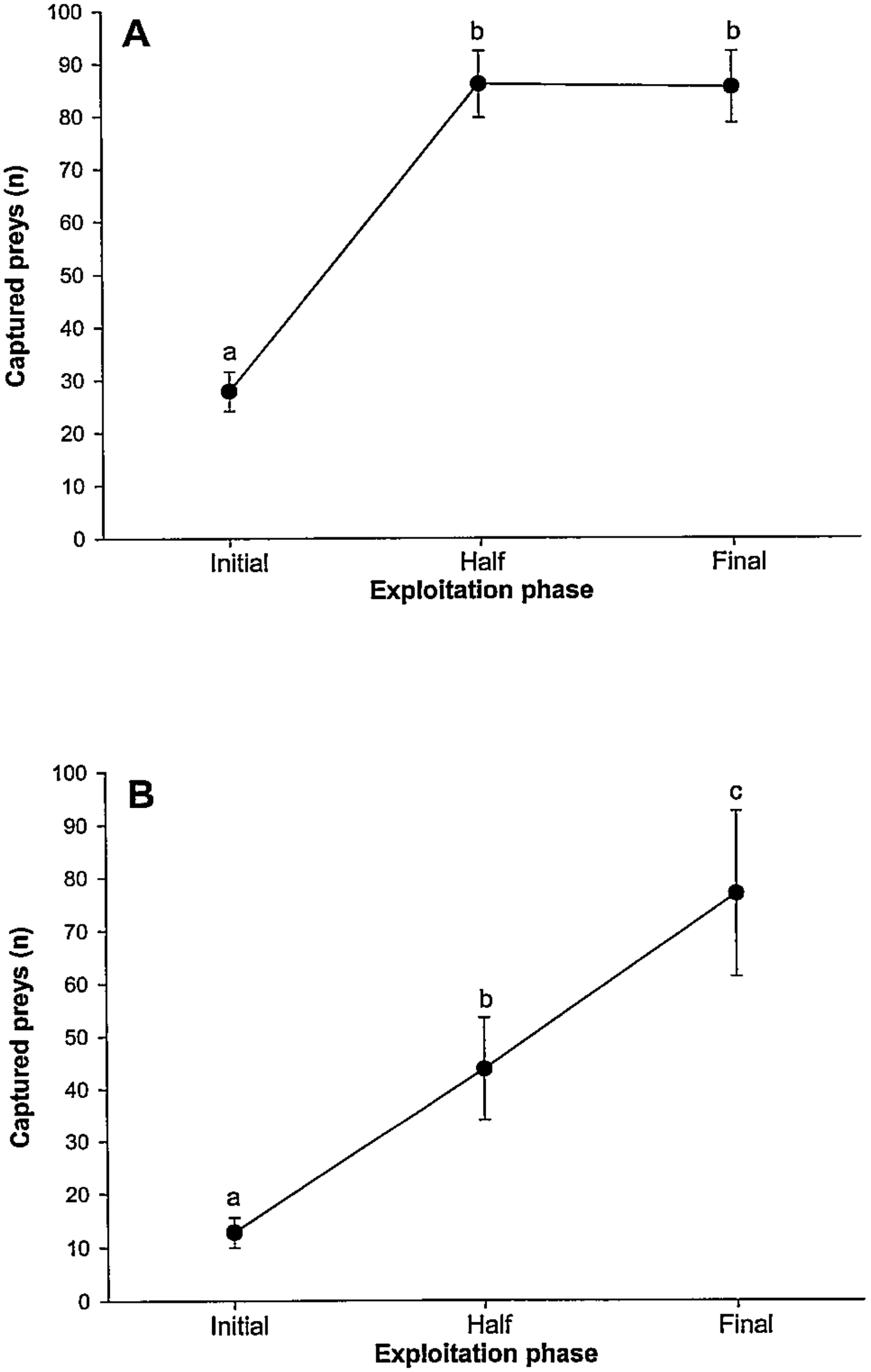
A
Captured preys (n)
100
90
80
70
60
50
40
30
20
10
0
a
b
b
Initial
Half
Final
Exploitation phase
B
Captured preys (n)
100
90
80
70
60
50
40
30
20
10
0
a
b
c
Initial
Half
Final
Exploitation phase

Figure 5

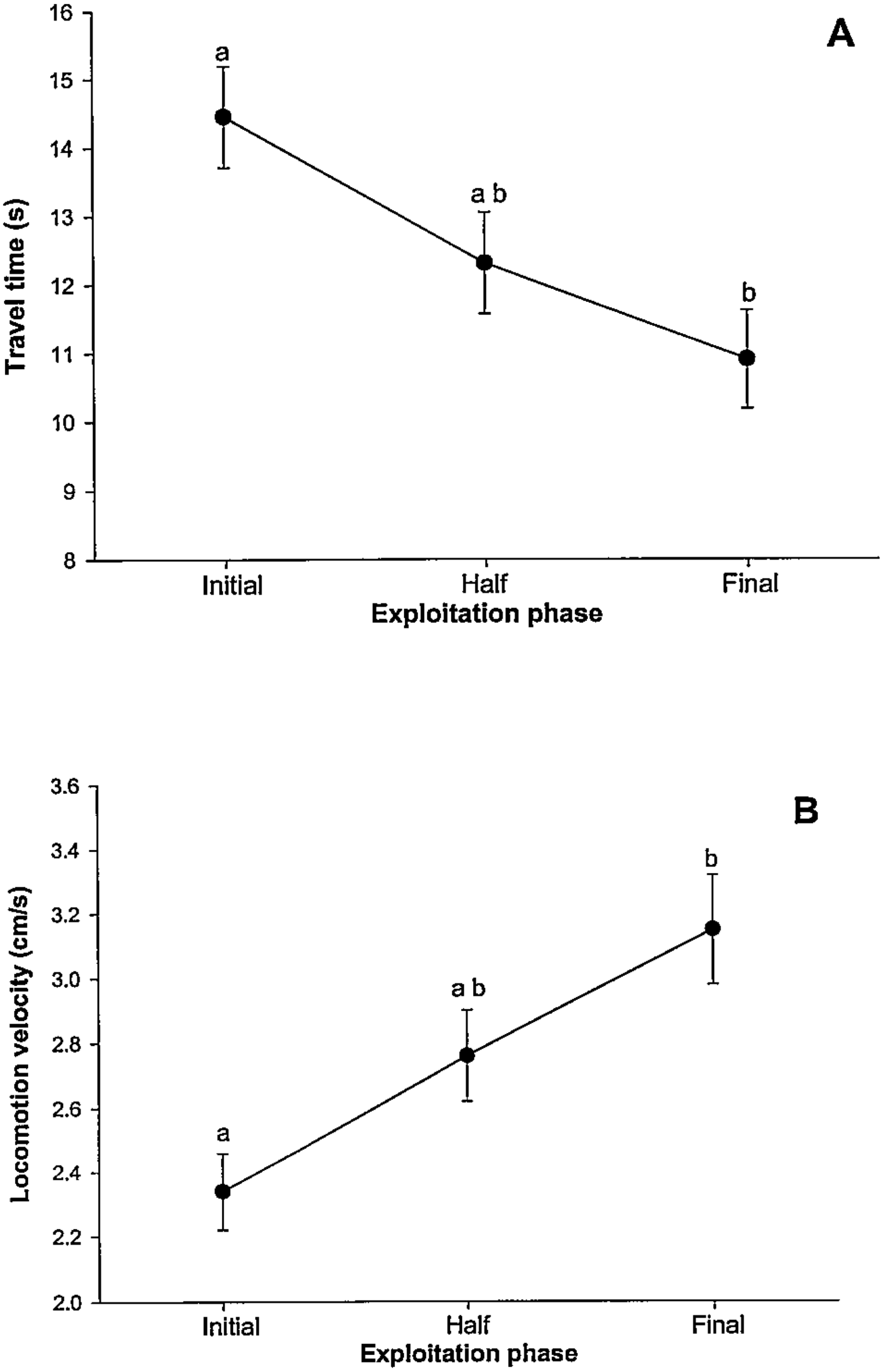
A
Travel time (s)
16
15
14
13
12
11
10
9
8
a
a b
b
Initial
Half
Final
Exploitation phase
B
Locomotion velocity (cm/s)
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
a
a b
b
Initial
Half
Final
Exploitation phase

Table 1. (A) Summary of the procedure and **(B)** results of a forward-stepwise multiple linear regression model on the effect of habitat and foragers variables on the resource removal rate of food patch located between 1-16 m from the nest entrance of *Pogonomyrmex barbatus* colonies.

(A) Procedure

Step	Variable entered	F	Significance	r^2 ajusted	R^2 change
1	Number foragers	9.815	0.0048	0.274	0.274
2	Head contacts	1.511	0.2319	0.315	0.041
3	Travel time	1.255	0.2747	0.349	0.034
4	Soil temperature	7.201	0.0136	0.504	0.155
5	Locomotion velocity	2.646	0.1180	0.557	0.053

(B) Results

Variable	Slope	Significance
Number foragers	0.082	0.0166
Head contacts	0.242	0.3687
Travel time	-0.777	0.0054
Soil temperature	-0.314	0.0326
Locomotion velocity	-1.782	0.1180
Constant	25.747	0.0025

Regression Model Summary: $R^2 = 0.44$; $F_{2,21} = 8.19$; $p < 0.01$

Table 2. (A) Summary of the procedure and **(B)** results of a forward-stepwise multiple linear regression model on the effect of habitat and foragers variables on the resource removal rate of food patch located between 1-4 m from the nest entrance of *Pogonomyrmex barbatus* colonies.

(A) Procedure

Step	Variable entered	F	Significance	r^2 ajusted	r^2 change
1	Number foragers	11.742	0.005	0.423	0.423
2	Spatial heterogeneity	2.608	0.132	0.508	0.085
3	Locomotion velocity	1.249	0.285	0.548	0.040
4	Soil temperature	14.585	0.002	0.786	0.238
5	Head contacts	4.596	0.053	0.845	0.059

(B) Results

Variable	Slope	Significance
Number foragers	0.143	<0.001
Spatial heterogeneity	1.680	0.250
Locomotion velocity	4.347	<0.01
Soil temperature	-0.632	<0.01
Head contacts	0.474	0.053
Constant	4.324	0.188

Regression Model Summary: $R^2 = 0.78$; $F_{5,12} = 13.21$; $p < 0.001$

Table 3. (A) Summary of the procedure and **(B)** results of a forward-stepwise multiple linear regression model on the effect of habitat and foragers variables on the resource removal rate of food patch located between 8-16 m from the nest entrance of *Pogonomyrmex barbatus* colonies.

(A) Procedure

Step	Variable removed	F	Significance	r^2 ajusted	r^2 change
1	Number of foragers	0.099	0.763	0.808	-0.006
2	Soil temperature	0.449	0.524	0.786	-0.021
3	Spatial heterogeneity	0.679	0.437	0.757	-0.029
4	Head contacts	1.331	0.286	0.704	-0.054

(B) Results

Variable	Slope	Significance
Travel time	-0.723	0.005
Locomotion velocity	-2.884	0.006
Constant	22.549	0.002

Regression Model Summary: $R^2 = 0.62$; $F_{2,7} = 8.31$; $p < 0.05$

CONCLUSIÓN GENERAL

Nuevos aportes.-

La ecología de paisaje ha analizado los efectos de la heterogeneidad espacial sobre la complejidad de las vías de movimiento de los individuos (e.g. With 1994, Wiens et al. 1995). Por otro lado, los estudios de forrajeo óptimo no han considerado explícitamente los tipos de trayectorias exhibidas por los organismos en la matriz entre parches de recursos, y por ende, no han analizado las consecuencias de la heterogeneidad del hábitat sobre el éxito de forrajeo (e.g. Charnov 1976, Orians & Pearson 1979, Pyke 1984). En esta tesis, ambos aspectos fueron integrados y constituyeron piezas fundamentales en el planteamiento de los objetivos. La importancia de abordar este tipo de problemática, de interés común para las disciplinas de la ecología de paisaje y conducta animal, había sido sólo sugerida implícitamente en estudios previos (e.g. Wiens et al. 1993, Ims 1995). En particular, esta tesis resalta tres aspectos novedosos que habían sido pasados por alto en la literatura. Primero, se definió el recurso alimento como el estímulo que genera los desplazamientos. Segundo, se analizaron los cambios temporales de las trayectorias de los individuos como resultado de la acumulación de información. Tercero, se evaluó la influencia del desempeño locomotor sobre el éxito de forrajeo de los organismos. Hasta la fecha no existen estudios que conecten en un protocolo común, estos tres elementos.

Los efectos de la estructura espacial del paisaje (véase hipótesis 1 y predicción 1) y la adquisición de información (véase hipótesis 2 y predicción 2) sobre el desempeño locomotor y éxito de forrajeo fueron evaluados en organismos forrajeadores de lugar central como las hormigas, mediante experimentos manipulativos de campo y laboratorio. Los experimentos de campo otorgaron un mayor realismo a los resultados encontrados y permitieron, a través de análisis estadísticos multivariados, ponderar la influencia simultánea de varios factores sobre la(s) conducta(s) de interés. En forma complementaria, los experimentos de laboratorio permitieron manejar y controlar las condiciones de unas pocas variables independientes y evaluar, de manera más precisa, los efectos de estos factores y sus interacciones sobre el desempeño conductual de organismos que fueron confrontados a diferentes tratamientos experimentales. A continuación, detallo brevemente las principales conclusiones acerca de la influencia de variables del paisaje y conductuales sobre la relación entre desempeño locomotor y éxito de forrajeo en hormigas.

Efecto de la heterogeneidad espacial de paisaje.-

En experimentos de laboratorio realizados con *Dorymyrmex goetschi* se encontró que una mayor varianza espacial en la distribución de obstáculos produjo un incremento significativo de los tiempos de viaje de retorno al nido y una disminución de las velocidades de locomoción (capítulo 3). Por el contrario, paisajes más heterogéneos produjeron un incremento de la velocidad de locomoción en *Camponotus chilensis* (capítulo 4).

Experimentos de campo efectuados con *D. goetschi* mostraron que una mayor heterogeneidad espacial de paisaje tendió a generar trayectorias con recorridos más largos (capítulo 1), viajes de ida y retorno con menores velocidades de locomoción (capítulo 2), menores intercambios de información (capítulo 1), y una menor tasa de remoción de presas por parte de la colonia (capítulo 1). De manera similar, la heterogeneidad del hábitat no tuvo efecto significativo sobre las conductas de locomoción y forrajeo en *Pogonomyrmex barbatus* (capítulo 5).

Durante la historia de vida de una colonia de hormigas, las obreras van incorporando información de su entorno (e.g. estructura del hábitat, presencia de potenciales competidores, distribución y abundancia de los recursos), lo cual determinaría que transcurrido cierto tiempo la heterogeneidad espacial de paisaje no tenga un efecto sobre las conductas de locomoción y forrajeo de los individuos. Los resultados de los experimentos de campo, donde no se manipuló la heterogeneidad espacial, son un reflejo de esto. Sin embargo, en un estado inicial (e.g. fundación de la colonia, perturbación ambiental, inicio de la temporada de forrajeo) los organismos se ven confrontados por primera vez a nuevas condiciones ecológicas y no tienen un conocimiento cabal de su entorno, por lo cual es probable que exista un efecto de las características físicas del hábitat sobre la conducta de las hormigas. Esta situación se corroboró en los experimentos de laboratorio donde se manipuló la heterogeneidad ambiental. De hecho, en la especie *D. goetschi* las condiciones abióticas de la estación de invierno (e.g. lluvia, nieve) y las perturbaciones de verano (e.g. antrópicas, fuego) pueden modificar las marcas familiares del paisaje utilizadas por las hormigas para su orientación visual durante los viajes de alimentación. De igual forma, en la especie *P. barbatus* las inusuales e intensas lluvias ("monsoon storms") producidas durante el verano pueden generar inundaciones que alteran la fisionomía del hábitat y modifican las marcas químicas depositadas por las obreras en las rutas de forrajeo.

Efecto de la adquisición de información.-

Los experimentos de campo realizados con *D. goetschi* mostraron que a mayor número de obreras y contactos antenales se produjo un incremento significativo del éxito de forrajeo de las colonias (capítulo 1). Además, las obreras que transportaban alimento al nido experimentaron una disminución de sus longitudes de recorrido con el transcurso del tiempo (capítulo 1). De igual forma, un mayor número de encuentros entre forrajeadoras de *P. barbatus* aumentó la tasa de remoción de recursos, a su vez, los tiempos de viaje disminuyeron, las velocidades de locomoción se incrementaron, y el número de presas capturadas aumentaron con el curso del tiempo (capítulo 5).

En el laboratorio, el número de obreras activas de *D. goetschi* incrementó con el paso del tiempo lo que se tradujo en un mayor número de contactos antenales y en un aumento significativo del éxito de forrajeo (capítulo 3). En las especies *Camponotus morosus* y *C. chilensis* se encontró el mismo tipo de relación entre encuentros cabeza a cabeza y presas capturadas, además de un incremento de las velocidades de locomoción en forrajeadoras de *C. chilensis* con el transcurso del tiempo (capítulo 4).

Previo a los tratamientos de laboratorio, las colonias fueron sometidas a "experimentos blanco" donde las hormigas accedían a una arena sin presencia de recursos y sus conductas fueron filmadas durante dos horas. Así por ejemplo, en *D. goetschi* sólo unas pocas obreras (1-5) exploraron el ambiente en distintas direcciones, estableciendo pocos contactos antenales entre sí, y no exhibiendo reclutamiento de compañeras de nido. Estos antecedentes resaltan dos aspectos. Primero, el alimento constituyó el estímulo que desencadenó los desplazamientos estudiados en los experimentos de laboratorio. Segundo, los contactos antenales constituyen un proceso de comunicación jerárquico, es decir, en una primera instancia permiten el reconocimiento entre individuos de una misma colonia, posteriormente la identificación de la tarea desempeñada por las obreras, y finalmente una toma de decisión específica (e.g. evaluación de la ubicación, calidad, y/o cantidad del alimento). Respecto al último paso, al no existir recursos en el ambiente, no ocurre transmisión de información sobre la necesidad de colectar alimento, y por ende no se presentan reclutamientos de individuos.

Relación entre desempeño locomotor y éxito de forrajeo.-

Los experimentos de laboratorio mostraron que una mayor velocidad de locomoción produjo un incremento del éxito de forrajeo en colonias de *D. goetschi* (capítulo 3). En *C. morosus* tiempos de viaje de corta duración implicaron un aumento del número de presas capturadas (capítulo 4).

En el trabajo de campo realizado con *D. goetschi* se encontró sólo una tendencia a que trayectorias de recorrido más corto produjeran una mayor tasa de remoción de recursos (capítulo 1). En cambio, en *P. barbatus* se encontró que la disminución del tiempo de viaje y el aumento de la velocidad de locomoción explicó un porcentaje significativo del incremento en desempeño de tareas de forrajeo (capítulo 5).

El esquema conceptual propuesto en la introducción general fue rechazado estadísticamente (véase Fig. 6a del capítulo 1). Este modelo inicial resultó ser demasiado simple y no consideró los efectos directos de la heterogeneidad espacial y uso de información sobre el éxito de forrajeo de los organismos. Estos consideraciones fueron incorporadas en un nuevo modelo que fue estadísticamente validado (véase Fig. 6c del capítulo 1). En este modelo, la heterogeneidad espacial y la complejidad de movimiento afectan a las variables respuesta en la dirección esperada por las hipótesis y predicciones, pero sólo el uso de información tiene un efecto significativo sobre la tasa de remoción de recursos de las colonias. Es decir, una colonia experimenta un incremento en el desempeño de forrajeo cuando procesa información y aumenta el conocimiento que tiene de su entorno. Es probable que los efectos del paisaje alcanzen un valor significativo si las colonias son estudiadas durante un estado inicial (e.g. primera semana de forrajeo), y que las vías de movimiento constituyan un factor clave cuando incorporan el eje temporal en su estimación (i.e. cuando se evalúa la velocidad de locomoción, véase e.g. capítulo 2).

Patrones generales.-

El grano de percepción corresponde a la capacidad de un organismo para reconocer discontinuidades en el ambiente, y por ende, de discriminar entre hábitats donde obtiene diferentes valores de adecuación biológica (*sensu* Levins 1968). Además, el concepto de grano hace referencia al tamaño del parche (véase pp. 18 en Levins 1968) y a la distancia entre parches (véase pp. 9 en Kolasa & Rollo 1991) presentes en el ambiente. Por tanto, el que un hábitat sea considerado grano fino o grueso constituye un problema de escala espacial que depende del nivel de percepción y tamaño corporal del organismo. De esta forma, si un organismo percibe todos los parches iguales y no efectúa un proceso de discriminación (e.g. desarrolla gran parte de su ciclo de vida en un sólo gran parche), entonces tiene un nivel de resolución de grano fino. En cambio, si un individuo es capaz de reconocer discontinuidades en el paisaje durante sus actividades diarias (e.g. trayectorias de forrajeo entre diferentes y pequeños parches de alimento), éste percibe el hábitat con grano grueso (*sensu* Levins 1968).

En particular, las hormigas perciben el ambiente con grano grueso. Estos insectos al poseer un tamaño corporal pequeño y extremidades alométricamente cortas, "caminan a través del paisaje" (Kaspari & Weiser 1999). De esta forma, las obreras son capaces de reconocer un gran número de intersticios ambientales (i.e. rugosidad ambiental) (Farji-Brener et al. 2004), y así explotar hábitats donde los recursos están distribuidos en forma parchosa (e.g. Kaspari 1993, Wiens et al. 1995). Este atributo sensorial explicaría el hecho que en los estudios de campo la heterogeneidad espacial, en el rango estudiado, no haya tenido un efecto significativo sobre el éxito de forrajeo de las colonias. Las especies de hormigas pueden usar diferentes tipos de señales de comunicación (e.g. visuales, químicas), lo cual les permite evadir obstáculos físicos, reconocer marcas familiares y/o orientar sus viajes en el paisaje (e.g. Collet 1996, Wehner et al. 1996). De esta forma, el efecto que la distribución espacial de objetos en experimentos de laboratorio tuvo sobre las trayectorias de *D. goetschi* y *C. chilensis*, se debería a los distintos tipos de información utilizada por estas especies. La utilización de criterios basados en reglas simples (e.g. tasa de encuentros con compañeras de nido) permiten a una obrera tomar decisiones sobre las tareas a ejecutar y su nivel de respuesta (e.g. Wilson & Hölldobler 1988, Gordon 1989, Gordon et al. 1993). El uso de estas reglas simples de decisión habría determinado los incrementos en desempeño locomotor y en remoción de recursos encontrados en esta tesis.

Finalmente, es importante destacar que el desempeño locomotor de obreras que tranportan alimento a un lugar central tiene una influencia directa sobre el éxito de forrajeo de la colonia, aspectos que habían sido tratados en forma independiente en la literatura. Sin duda, un ahorro de los costos de tiempo y energía involucrados en la ejecución de estas actividades, tendría un efecto positivo sobre la adecuación biológica de los organismos. En particular, un aspecto relevante de los resultados corresponde al patrón general encontrado para especies de hormigas que diferían en las escalas espaciales de sus desplazamientos (e.g. 0.5 m *versus* 16.0 m), hábitos tróficos (e.g. granívoros estrictos *versus* generalistas), y la estrategia utilizada para explotar los recursos (e.g. forrajeo individual *versus* en grupo).

Proyecciones.-

Como se desprende de los efectos moduladores de la ecología de paisaje y conducta animal, y las conexiones establecidas entre ambos marcos teóricos, el énfasis de esta tesis estuvo puesto en el estudio de efectos y relaciones entre movimiento y forrajeo en insectos sociales como las hormigas. Por lo tanto, un siguiente paso sería estudiar los mecanismos de comunicación utilizados por estos organismos durante la expresión de estas conductas.

Cuando una hormiga abandona el nido para explotar un parche de recursos, ésta debe ser capaz de utilizar señales que le permitan orientar sus viajes de ida y regreso (Traniello & Robson 1995). Diversas modalidades sensoriales (e.g. visuales, táctiles, acústicas, químicas) permiten la transmisión de información entre las obreras (Hölldobler 1984, Hölldobler & Wilson 1990, Dusenbery 1992, Gordon et al. 1993). En especies que forrajean de forma individual, el sistema visual le permite a una hormiga reconocer, mientras se desplaza, marcas familiares existentes en el paisaje (e.g. ubicación relativa del nido, piedras, arbustos) y/o señales en el cielo (e.g. posición del sol, patrón de luz polarizada) (Wehner 1996, Collet et al. 1998, Nicholson et al. 1999, Schatz et al. 1999). En especies que forrajean en grupo, el reclutamiento y orientación de las obreras está determinado esencialmente por la producción de señales químicas conocidas como feromonas de camino (e.g. Hölldobler & Wilson 1990, Gordon 1994).

Las feromonas de camino en la especie *P. barbatus* son producidas en las glándulas de veneno y de Dufour (e.g. Hölldobler et al. 2001, 2004), en especies del género *Camponotus* en la glándula del intestino posterior (e.g. Bestmann et al. 1995, Übler et al. 1995, Haak et al. 1996, Kohl et al. 2001, 2003), y en hormigas de la subfamilia Dolichoderinae en las glándulas de Pavan y pigidial (e.g. Robertson et al. 1980, Hölldobler & Wilson 1990, Simon & Hefetz 1991, Attygale et al. 1998). Estas sustancias son liberadas cuando las hormigas bajan y arrastran la punta del abdomen en el sustrato. Posteriormente, estas señales químicas van siendo remarcadas por las obreras, son usadas para orientar los viajes de las forrajeadoras, y determinan la expresión de un trabajo colectivo durante la búsqueda y colecta de alimento. Además, en hormigas granívoras (e.g. Wagner et al. 1998, 2000, 2001) y carpinteras (e.g. Bonavita-Cougourdan et al. 1993, Meskali et al. 1995, Boulay et al. 2000, Errard et al. 2003) se ha documentado que las obreras son capaces de discriminar la tarea ejecutada por una compañera de nido con la cual establecen contacto antenal, a partir del reconocimiento químico de los hidrocarburos de cutícula, lo cual incrementa el desempeño de ciertas actividades como el forrajeo.

Si bien las señales químicas son los canales de comunicación mejor estudiados en hormigas, existen modalidades sensoriales accesorias (e.g. estímulos vibratorios, táctiles) que juegan un importante papel en la generación de señales multimodales, las cuales incrementan el intercambio de información entre hormigas (e.g. Hölldobler 1995, 1999). Esencialmente, la integración de diversos tipos de señales permite modular la transferencia de información, y de esta forma, disminuir el umbral de respuesta de los individuos receptores frente a la constante liberación de estímulos por parte de los emisores (e.g. Hölldobler 1995, 1999). Por lo tanto, no se debe descartar la participación de otro tipo de señales como las visuales y/o acústicas (e.g. Klotz & Reid 1993, Rohe & Rupprecht 2001), como mecanismos de comunicación responsables de las conductas de locomoción y forrajeo exhibidas por las especies de hormigas aqui estudiadas. En resumen, el estudio de aspectos mecanicistas, en especial los que dicen relación con la comunicación química entre obreras, permitirá profundizar, complementar y extender los trabajos sobre conductas de locomoción y forrajeo en hormigas.

A parte de las hormigas, existen otros insectos sociales (e.g. abejas, avispas, termitas) así como vertebrados sociales (e.g. ratas, ardillas, estorninos) que son forrajeadores de lugar central, donde también se ha observado variabilidad en las conductas de forrajeo. Para este tipo de organismos la adquisición de información respecto a las características espaciales del paisaje también jugaría un papel clave en el desempeño de sus conductas de locomoción y alimentación, ya que les permitiría monopolizar presas, minimizar tiempos de viaje, e incrementar la tasa de remoción de recursos. Además, si los individuos son capaces de establecer interacciones de tipo cooperativo (e.g. eventos de reclutamiento) se generarán estrategias de trabajo colectivo para explorar y explotar los parches de alimento presentes en el ambiente. Esta serie de acontecimientos se traducirá en ahorros de tiempo, que les permitirán a los organismos realizar otras actividades tales como construcción de nidos, conductas antidepredatorias, búsqueda de parejas reproductivas, y/o cuidado de progenie, entre otras, lo cual finalmente se reflejará en una mayor adecuación biológica.

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ANEXO

Antecedentes biológicos de hormigas presentes en Chile publicados en revistas científicas nacionales y extranjeras durante el siglo XX

RESUMEN

Se revisa la información sobre biología de hormigas presentes en Chile publicada en revistas científicas nacionales y extranjeras durante el período 1900-1999. Se evalúan estos antecedentes en términos de: i) la dinámica temporal de la producción de publicaciones, ii) las principales temáticas de estudio, y iii) los géneros de formícidos en los cuáles se ha concentrado la investigación. Los datos recolectados muestran que sólo a partir de la década del 60' se produce un marcado crecimiento del número de artículos sobre hormigas, lo cual alcanza su máxima expresión durante la década del 90'. Los principales tópicos de investigación han sido, en orden decreciente, aspectos sobre taxonomía, uso del hábitat, períodos de actividad, conductas tróficas y de reconocimiento entre individuos. Los géneros de formícidos en los que se han centrado estos estudios corresponden a *Camponotus*, *Solenopsis*, *Pogonomyrmex*, *Brachymyrmex*, *Conomyrma* y *Linepithema*. Estos resultados son discutidos a la luz de acontecimientos históricos que habrían determinado el curso de las investigaciones. Finalmente, se proponen líneas de investigación que en el futuro podrían desarrollar los estudios sobre hormigas en Chile.

Palabras claves: hormigas, Chile, ecología, taxonomía, *Camponotus*, *Solenopsis*

INTRODUCCIÓN

Existen aproximadamente 8.800 especies conocidas de hormigas en el mundo, las cuales dominan una variedad de hábitats y ambientes ecológicos, donde alcanzan una gran abundancia (Holldobler & Wilson 1990). Las hormigas constituyen el principal grupo de insectos eusociales, los cuáles se caracterizan por presentar: i) individuos adultos que cooperan en la construcción del nido y el cuidado de la progenie, ii) división de la labor reproductiva, con individuos estériles que trabajan a favor de la fecundidad del nido, y iii) sobreposición de generaciones, las cuáles son capaces de contribuir a las tareas de la colonia (Seger 1991, Bourke 1997). Una característica distintiva de las hormigas es que presentan tres castas morfológicas de sexo femenino - obreras, soldados y reinas – y una casta de individuos machos que cumple una breve función reproductiva durante el vuelo nupcial (Wilson 1971, Oster & Wilson 1978). En una colonia, la casta obrera es la que desempeña una mayor variedad de tareas como por ejemplo, forrajeo, cuidado de progenie y construcción de nidos (Wilson 1985, Gordon 1996).

Otra característica importante de las hormigas es su haplodiploidía, debido a lo cual los huevos no fertilizados se desarrollan en machos haploides y los huevos fertilizados en hembras diploides (Heinrich 1978, Brockman 1984). El modo en que se determina el sexo favorece la selección por parentesco, en la cual la proporción de genes compartidos por las obreras condiciona el cuidado de la progenie de sus hermanas (altruismo reproductivo), de forma tal que aseguran indirectamente a través de sus parientes una mayor representación o inversión futura de sus genes en la población (fitness inclusivo), en comparación a si estos individuos produjeran su propia descendencia (Hamilton 1964, Trivers & Hare 1976, Krebs & Davies 1993). Existen además una serie de atributos como por ejemplo, fundación de colonias a partir de una o más reinas, comunicación química (feromonas) entre obreras, movimientos de forrajeo en solitario y/o en columna, y relaciones simbióticas con otras especies de hormigas, insectos y plantas, que convierten a las hormigas en interesantes objetos de estudio (Holldobler & Wilson 1990).

En Chile existen 62 especies de hormigas, las cuáles se distribuyen en 22 géneros, los que a su vez están adscritos a cinco subfamilias (Ponerinae, Pseudomyrmecinae, Myrmicinae, Dolichoderinae, Formicinae) (Snelling & Hunt 1975, Rojas & Elgueta 1995). La riqueza de formícidos en Chile es pobre en comparación a la fauna mirmecológica de Sudamérica, incluye 10 especies consideradas como hormigas introducidas, 4 con distribución neotropical, 14 con distribución patagónica, y 34 especies endémicas (Snelling & Hunt 1975). Sólo en las últimas dos décadas se han realizado trabajos que han abordado en profundidad aspectos de la ecología de las hormigas presentes en Chile; sin embargo, existe una escasez de conocimiento en muchas temáticas. El objetivo de este trabajo fue recopilar información relevante sobre la biología de hormigas en Chile presente en revistas científicas extranjeras y – especialmente – nacionales durante el período 1900-1999. Se analiza esta información en términos de: i) la dinámica temporal de la producción de publicaciones, ii) las principales temáticas de estudio, y iii) los géneros de formícidos en los cuáles se ha concentrado la investigación. Los resultados son discutidos a la luz de acontecimientos históricos que habrían determinado el curso de las investigaciones. Finalmente, se proponen líneas de investigación que en el futuro podrían desarrollar los estudios sobre hormigas presentes en Chile.

METODOLOGÍA

Se revisaron los catálogos de revistas científicas nacionales publicados por M. Etcheverry en la Revista Chilena de Historia Natural a partir de 1985, y se actualizó y completó la búsqueda bibliográfica hasta el año 1999 inclusive. Las principales revistas consultadas fueron: 1) Acta Entomológica (1985-1999), 2) Actas de la Societé Scientifique du Chili (1891-1971), 3) Anales de la Academia Chilena de Ciencias Naturales (1926-1968), 4) Anales del Museo de Historia Natural de Valparaíso (1968-1999), 5) Anales del Instituto de la Patagonia (Ciencias Naturales) (1970-1999), 6) Anales del Museo Nacional de Historia Natural (1891-1910), 7) Anales de Zoología

Aplicada (1914-1922), 8) Boletín del Museo Nacional de Historia Natural (1908-1999), 9) Boletín del Museo Regional de Concepción (1926-1999), 10) Boletín de la Sociedad de Biología de Concepción (1927-1999), 11) Bosque (1975-1998), 12) Gayana (Zoología) (1961-1999), 13) Investigaciones Zoológicas Chilenas (1950-1964), 14) Medio Ambiente (1975-1996), 15) Noticiario Mensual del Museo Nacional de Historia Natural (1956-1999), 16) Publicaciones del Centro de Estudios Entomológicos (1960-1974), 17) Publicación Ocasional del Museo Nacional de Historia Natural (1963-1992), 18) Revista Chilena de Entomología (1951-1999), y 19) Revista Chilena de Historia Natural (1897-1999).

En relación a las publicaciones sobre hormigas en Chile presentes en revistas científicas extranjeras, se realizó una búsqueda bibliográfica en la base de datos BIOSIS durante el período comprendido entre 1985-2000. En forma paralela, esta búsqueda fue complementada con la base de datos CAB Abstracts (INIA), lo cual permitió cubrir los años 1972-2000. En ambos casos se utilizaron como palabras claves, términos lo más amplios y generales posibles (e.g. Hymenoptera, ant(s), Chile). Es importante mencionar que tanto en el caso de publicaciones nacionales y extranjeras, parte de la información – en especial aquella referida a trabajos anteriores a la década del 70' - fue obtenida a partir de una minuciosa revisión de la bibliografía y/o referencias citada en los trabajos de que se disponía. Los nombres taxonómicos de las especies de hormigas mencionadas en la sección resultados y discusión han sido actualizados según el catálogo de Snelling & Hunt (1975) y corroborados con la reciente revisión de Rojas & Elgueta (1995); entre este lapso de tiempo destaca la nueva sinonimia del género *Conomyrma* Forel (= *Araucomyrmex* Gallardo) propuesta por Snelling (1981) y la nueva combinación de *Linepithema humile* (Mayr) (= *Iridomyrmex humilis*) propuesta por Shattuk (1992). En resultados y discusión me referiré en forma general a hormigas chilenas; este término agrupa tanto a las especies nativas como a las introducidas (estas últimas serán destacadas con un asterisco (*) en el texto, figuras y tabla).

RESULTADOS

Las primeras informaciones respecto a hormigas chilenas, se remontan a mediados del siglo XIX y corresponden esencialmente a antecedentes taxonómicos. El trabajo pionero de Spinola (1851) publicado en la clásica obra "Historia física y política de Chile" de C. Gay documenta la existencia de siete especies de formícidos (*Camponotus distinguendus*, *C. chilensis*, *C. ovaticeps*, *Lasiophanes nigriventris*, *Pseudomyrmex lynceus*, *Solenopsis gayi*, y *Pogonomyrmex bispinosus*). Posteriormente, el trabajo de Berg (1890) recopila antecedentes documentados por autores como A. Forel, F. Smith, J. Roger y esencialmente G. Mayr, reportando la presencia de 23 especies así como algunos comentarios sobre la biología de estas especies. A similar resultado llega un trabajo de Emery (1894) donde se describen dos nuevas especies (*Brachymyrmex giardii* y *B. laevis*), posteriormente este mismo autor (Emery 1895) documenta a cinco nuevas especies (*Nothidris latastei*, *Solenopsis germaini*, *S. helena*, *S. latastei*, y *Conomyrma minutus*) y sus lugares de recolección.

Dinámica temporal de producción de publicaciones

Durante el siglo XX existen 58 publicaciones que entregan antecedentes biológicos sobre la fauna mirmecológica de Chile. A continuación se detalla de manera parcelada el curso seguido por la producción de artículos sobre hormigas chilenas durante las diferentes décadas (Fig. 1). En esta cuantificación no se incluyen trabajos referentes a biología de hormigas chilenas presentes en islas oceánicas, debido a la escasa información existente respecto al tema (Wheeler 1923, Kuschel 1957, Campos & Peña 1973, Peña 1987). Por otra parte, cuando es pertinente se hace mención a antecedentes sobre hormigas foráneas publicados en revistas científicas nacionales.

Período 1900-1909: En este período no existe información sobre hormigas chilenas. Sin embargo, Gallardo (1908) publica un artículo en la Revista Chilena de Historia Natural sobre la fundación de colonias de "hormigas sauvá y negra" (*Atta* sp.), y su alimentación y mantención a partir de cultivo de hongos.

Período 1910-1919: En este período tampoco existe información sobre hormigas chilenas. A pesar de esto, se publican en revistas nacionales tres pequeñas notas sobre cultivo de hongos, daño a cultivos agrícolas y vida en simbiosis con orugas, por parte de hormigas foráneas (Porter 1910, La Redacción 1914, Porter 1915).

Período 1920-1929: Durante este período existen dos artículos en los que se hace mención a hormigas chilenas. Una publicación se refiere a la presencia de formícidos (*Tetramorium caespitum**, *Lasiophanes valdiviensis*, *Brachymyrmex giardii*) en la región mediterránea y sur de Chile (Santschi 1922), y la otra a la diagnosis de especies (*Solenopsis gayi*, *S. patagonica*, *Tapinoma antarcticum*) reportadas también por Santschi en estas mismas regiones (Porter 1923b). En forma paralela, se publican en revistas nacionales tres pequeñas notas sobre parasitismo de colmenas de abejas, coexistencia con Bracónidos y depredación de piojos, por parte de hormigas foráneas (Wolffsohn 1920, Porter 1923a, 1926).

Período 1930-1939: Durante este período se produjeron cinco artículos sobre hormigas chilenas. Un par de publicaciones analiza la comunicación química y conductas asociadas de exploración y orientación del movimiento en obreras de *Solenopsis gayi* y *Pogonomyrmex bispinosus* (Goetsch 1930a, 1930b). Por otra parte, tres trabajos entregan antecedentes taxonómicos sobre el número de formícidos presentes en Chile. Es así como Goetsch (1933) documenta la existencia aproximada de 34 especies, y el trabajo de Menozzi (1935) y su posterior traducción al alemán por parte de Goetsch & Menozzi (1935) reportan la existencia de 56 especies, destacando el registro de tres nuevas especies (*Conomyrma goetschi*, *Myrmelachista goetschi* y *Camponotus hellmichi*). Finalmente, un artículo publicado en los Anales de la Academia Chilena de Ciencias Naturales documenta procedimientos para exterminar hormigas y evitar así los daños provocados en la agricultura (Pérez-Canto 1937).

Período 1940-1949: De acuerdo a la búsqueda y revisión efectuada en este trabajo, durante esta década no se registran publicaciones que contengan información relevante sobre hormigas chilenas, ni tampoco antecedentes generales sobre formícidos foráneos que hayan sido documentados en revistas científicas nacionales.

Período 1950-1959: El trabajo de Kusnezov (1959) corresponde al único antecedente publicado durante esta década, que hace mención a hormigas chilenas. Este artículo trata aspectos taxonómicos de formícidos que se distribuyen en el oeste de la Patagonia y Tierra del Fuego, e incluye importantes comentarios acerca de la biología de estas especies. Específicamente, este autor documenta para esta región hormigas pertenecientes a los géneros *Solenopsis* (*S. patagonica*), *Antichthonidris* (*A. bidentatus, A. denticulatus*), *Pogonomyrmex* (*P. angustus, P. laevigatus, P. odoratus*), *Conomyrma* (*C. antarcticus, C. tener*), *Lasiophanes* (*L. nigriventris, L. picinus*) y *Camponotus* (*C. chilensis, C. distinguendus*), los cuáles se presentan esencialmente asociados a bosques de *Nothofagus*, coníferas (araucarias, cipreces de las guaitecas), alerces y mañios.

Período 1960-1969: En este período se producen cuatro trabajos sobre hormigas de Chile. De éstos, tres corresponden a temáticas taxonómicas, destacando el trabajo sobre zoogeografía de hormigas Sudamericanas de Kusnezov (1963), quien basado en el trabajo de Goetsch & Menozzi (1935) y colecciones de T. Cekalovic en el extremo sur del país (provincia de Magallanes), dedica una sección a la fauna mirmecológica de Chile. En este trabajo el autor determina un total aproximado de 43 especies, entrega antecedentes sobre las localidades de recolección, compara su diversidad y riqueza con las faunas de Norte América, Patagonia, Australia y Nueva Zelandia, y discute los tiempos de evolución y posibles centros de origen de las especies. El otro par de publicaciones abordan aspectos taxonómicos de los géneros *Pogonomyrmex* (específicamente de *P. vermiculatus* en la región de Magallanes; Cekalovic 1964), y *Nothidris* (esencialmente de *N. bicolor* en la región de Coquimbo; Ettershank 1965). Finalmente, Ipinza-Regla (1969) discute el papel de *Solenopsis gayi* como modificador del paisaje correspondiente a la sabana espinosa chilena.

Período 1970-1979: Durante este período se publicaron 11 artículos sobre hormigas chilenas. Entre éstos, destacan el trabajo de Kempf (1970, 1972) que corresponde a la elaboración de un catálogo de formícidos chilenos en el cual se reportan 52 especies, y el documento de Snelling & Hunt (1975) el cual consiste en una clave taxonómica para la identificación de 62 especies de hormigas presentes en Chile, y contiene además valiosos datos sobre sus rangos de distribución y comentarios acerca de su biología. Previo a este documento, un par de trabajos había documentado el patrón temporal de actividad en las especies competidoras *Conomyrma antarcticus* y *Tapinoma antarcticum* (Hunt 1974), y el reporte de las siguientes nuevas especies: *Nothidris cekalovici*, *Solenopsis dysderces*, *Dorymyrmex agallardoi*, *Conomyrma hunti*, *C. hypocritus*, *C. incomptus*, *C. pappodes*, y *C. pogonius* (Snelling 1975). Finalmente, durante estos años también se publicaron algunos artículos sobre la generación de cuadros anafilácticos por la "picadura" de *Heteroponera carinifrons* (Ipinza & Capurro 1972, Ipinza & Schenone 1972), abundancia de formícidos en la sabana espinosa en relación a variables abióticas (Ipinza-Regla 1971a, 1971b), y la presencia de *Solenopsis gayi* en la dieta de *Pitius pitius* (Ave, Picidae) (Moroni 1977) y de especies de *Camponotus* en la dieta de *Liolaemus monticola* (Reptilia, Iguanidae) (Fuentes & Ipinza 1979).

Período 1980-1989: Durante esta década también se produjeron 11 artículos sobre hormigas chilenas, pero además se publicaron en revistas nacionales dos trabajos sobre formícidos foráneos, uno relacionado con hormigas cortadoras de hojas paraguayas y el otro referente a comunidades de hormigas del mato grosso brasileño (Fowler 1981, 1988). En lo que respecta a la información nacional, destacan los trabajos sobre distribución de especies de formícidos - de las subfamilias Mirmicinae y Dolichoderinae - en relación a los tipos de hábitats y condiciones bioclimáticas que ocupan (Ipinza-Regla & Covarrubias 1982, 1989), y distribución espacial de nidos de hormigas en gradientes altitudinales de sectores precordilleranos de Chile central (Ipinza-Regla et al. 1983, 1986, Covarrubias et al. 1987). Por otra parte, en este período también se documentó información sobre el efecto de depredadores, conductas tróficas y períodos de actividad de *Camponotus morosus* (Ipinza-Regla 1985, Grez et al. 1986, Ipinza-Regla et al. 1988), así como el rol desempeñado como vector de infecciones bacteriológicas intrahospitalarias y vector de contaminación microbiana en industrias de alimentos, por parte de *Linepithema humile** (Ipinza-Regla et al. 1981, 1984). Finalmente, un trabajo discute el efecto perjudicial indirecto que *Linepithema humile** ocasiona a cultivos agrícolas (Ripa 1987).

Período 1990-1999: Esta década constituye sin duda la etapa más productiva de publicaciones sobre hormigas chilenas, registrándose un total de 24 artículos. Entre estos trabajos destacan los estudios sobre ensambles de hormigas granívoras (*Conomyrma goetschi, Brachymyrmex giardii, Solenopsis gayi,* y *Pogonomyrmex vermiculatus*), donde se discute su efecto en la generación de patrones y procesos a nivel comunitario (Medel & Vásquez 1994, Medel 1995, Medel & Fuentes 1995, Vásquez et al. 1995, Fuentes et al. 1996). Durante este período también se analizó el nivel de "hermetismo" que presentan sociedades homo y/o heteroespecíficas de hormigas (*Camponotus morosus, C. chilensis, Brachymyrmex giardii, Solenopsis gayi*), determinándose el tiempo de latencia y orden en que se presentan ciertas unidades conductuales (e.g. exploración antenal, abertura mandibular, flexión del abdomen) que permiten el reconocimiento y aceptación entre individuos (Ipinza-Regla et al. 1991, 1993b, 1994, 1996, 1998, Ipinza-Regla & Morales 1998). En un siguiente orden de importancia, destacan los trabajos relacionados con problemáticas de uso del hábitat por parte de distintas especies de hormigas; específicamente asociación a diferentes tipos de hábitats (Solervicens et al. 1991, Lewis & Peredo 1993), capacidad de recuperación poblacional frente a una perturbación del hábitat (Saiz & Carvajal 1990), y distribución espacial de nidos (Ipinza-Regla et al. 1990). Por otra parte, algunos artículos documentan el efecto negativo de *Linepithema humile** y *Solenopsis gayi* sobre árboles frutales (Ripa et al. 1993a, 1993b, Larraín et al. 1995, Ripa et al. 1998). Además, un trabajo evaluó la conducta de "atención" de áfidos por parte de *Linepithema humile** cuando ésta es expuesta a compuestos volátiles (semioquímicos) involucrados en la conducta de espaciamiento de estos áfidos (Córdova-Yamauchi et al. 1998). Finalmente, para especies pertenecientes al género cosmopolita *Camponotus* se documentan antecedentes acerca de sus conductas tróficas (Ríos-Aramayo & Jiménez 2000), ámbito de hogar (Ipinza-Regla et al. 1993a), genética de colonias (Eaton & Medel 1994), y notas técnicas (Ipinza-Regla et al. 1992).

Principales temáticas de estudio

Los principales tópicos de investigación sobre hormigas chilenas desarrollados durante el siglo XX se muestran en la Fig. 2 y Tabla 1. Es importante mencionar que una publicación puede haber analizado más de una temática, y por ende ésta fue considerada un aporte de antecedentes en varias categorías de estudio. Entre la totalidad de artículos, destacan claramente los trabajos sobre taxonomía, los cuáles registraron una producción de 10 publicaciones durante el período 1900-1999 (Porter 1923, Goetsch 1933, Kusnezov 1959, 1963, Cekalovic 1964, Ettershank 1965, Kempf 1970, 1972, Snelling 1975, Snelling & Hunt 1975).

En otro ámbito, sobresalen trabajos relacionados con ejes que definen el nicho ecológico en animales; esencialmente éstos corresponden a nueve artículos referidos al uso del hábitat (Ipinza 1971b, Ipinza-Regla & Covarrubias 1982, Ipinza-Regla et al. 1983, 1986, Covarrubias et al. 1987, Ipinza-Regla & Covarrubias 1989, Ipinza-Regla et al. 1990, Solervicens et al. 1991, Lewis & Peredo 1993); ocho estudios sobre períodos de actividad (Ipinza-Regla 1969, 1971a, Hunt 1974, Ipinza-Regla et al. 1988, Medel & Vásquez 1994, Medel & Fuentes 1995, Fuentes et al. 1996, Ríos-Aramayo & Jiménez 2000); y siete publicaciones relacionadas a conductas tróficas de las hormigas (Grez et al. 1986, Medel & Vásquez 1994, Medel 1995, Medel & Fuentes 1995, Vásquez et al. 1995, Fuentes et al. 1996, Ríos-Aramayo & Jiménez 2000). Muy relacionado al último tópico, figuran cinco estudios comunitarios sobre patrones ecológicos de ensambles de hormigas granívoras (Medel & Vásquez 1994, Medel 1995, Medel & Fuentes 1995, Vásquez et al. 1995, Fuentes et al. 1996), y cuatro trabajos que analizan la trayectoria de los movimientos de forrajeo exhibidos por obreras entre el nido de la colonia y sus fuentes de alimento (Goetsch 1930a, 1930b, Ipinza-Regla et al. 1993a, Medel & Fuentes 1995).

Por otra parte, también se publicaron seis artículos sobre conductas de reconocimiento entre individuos (Ipinza-Regla et al. 1991, 1993b, 1994, 1996, 1998, Ipinza-Regla & Morales 1998), cinco trabajos sobre daños producidos a árboles frutales (Ripa 1987, Ripa et al. 1993a, 1993b, Larraín et al. 1995, Ripa et al. 1998), y cuatro artículos sobre el efecto de la depredación y/o perturbación sobre distintas especies de formícidos (Moroni 1977, Fuentes & Ipinza 1979, Ipinza-Regla 1985, Sáiz & Carvajal 1990). Finalmente, cuatro trabajos analizaron el papel de las hormigas como vectores de enfermedades y/o productores de cuadros anafilácticos (Ipinza & Capurro 1972, Ipinza & Schenone 1972, Ipinza-Regla et al. 1981; 1984), y tres artículos fueron clasificados en la categoría de varios (Ipinza-Regla et al. 1992, Eaton & Medel 1994, Córdova-Yamauchi et al. 1998).

Géneros de formícidos en los que se ha concentrado la investigación

Los principales géneros de hormigas chilenas en los cuáles se realizaron estudios durante el siglo pasado se muestran en la Fig. 3 y Tabla 1. En este catastro no se incluyeron los trabajos que constituyen claves y/o listas taxonómicas de especies de formícidos (i.e. Goetsch 1933, Kusnezov 1959, 1963, Kempf 1970, 1972, Snelling & Hunt 1975). Los resultados muestran que en 22 artículos existe información referida al género cosmopolita *Camponotus* (Ipinza 1971b, Fuentes & Ipinza 1979, Ipinza-Regla et al. 1983, Ipinza-Regla 1985, Grez et al. 1986, Ipinza-Regla et al. 1986, Covarrubias et al. 1987, Ipinza-Regla et al. 1988, 1990, Sáiz & Carvajal 1990, Solervicens et al. 1991, Ipinza-Regla et al. 1991, 1992, 1993a, 1993b, Lewis & Peredo 1993, Eaton & Medel 1994, Ipinza-Regla et al. 1994, 1996, 1998, Ipinza-Regla & Morales 1998, Ríos-Aramayo & Jiménez 2000), y que en 20 trabajos se abordan aspectos biológicos del género *Solenopsis* (Porter 1923, Goetsch 1930a, 1930b, Ipinza-Regla 1969, 1971b, Snelling 1975, Moroni 1977, Ipinza-Regla & Covarrubias 1982, Ipinza-Regla et al. 1983, Covarrubias et al. 1987, Ipinza-Regla et al. 1990, Sáiz & Carvajal 1990, Solervicens et al. 1991, Medel & Vásquez 1994, Medel 1995, Medel & Fuentes 1995, Larraín et al. 1995, Fuentes et al. 1996, Ipinza-Regla et al. 1996, Ripa et al. 1998); constituyendo estos los dos principales géneros de hormigas en los cuales se ha concentrado la investigación.

En una siguiente categoría de importancia, aparecen el género *Pogonomyrmex* con 11 publicaciones (Goetsch 1930a, 1930b, Cekalovic 1964, Ipinza 1971b, Ipinza-

Regla & Covarrubias 1982, Ipinza-Regla et al. 1983, Ipinza-Regla 1985, Covarrubias et al. 1987, Sáiz & Carvajal 1990, Solervicens et al. 1991, Medel & Fuentes 1995), el género *Brachymyrmex* con 10 artículos (Ipinza 1971b, Ipinza-Regla et al. 1983, Ipinza-Regla 1985, Covarrubias et al. 1987, Ipinza-Regla et al. 1990, Solervicens et al. 1991, Ipinza-Regla et al. 1994, Medel & Vásquez 1994, Medel 1995, Fuentes et al. 1996), y el género *Conomyrma* también con 10 trabajos (Hunt 1974, Snelling 1975, Ipinza-Regla et al. 1983, Covarrubias et al. 1987, Ipinza-Regla & Covarrubias 1989, Ipinza-Regla et al. 1990, Solervicens et al. 1991, Medel & Vásquez 1994, Medel 1995, Fuentes et al. 1996). En otro orden, existe información del género *Linepithema** en 10 artículos (Ipinza 1971b, Ipinza-Regla et al. 1981, 1984, Ipinza-Regla 1985, Ripa 1987, Ipinza-Regla & Covarrubias 1989, Ripa et al. 1993a, 1993b, 1998, Córdova-Yamauchi et al. 1998), antecedentes del género *Tapinoma* en seis publicaciones (Porter 1923, Ipinza 1971b, Hunt 1974, Ipinza-Regla & Covarrubias 1989, Sáiz & Carvajal 1990, Solervicens et al. 1991), datos sobre el género *Nothidris* en cuatro trabajos (Ettershank 1965, Snelling 1975, Ipinza-Regla & Covarrubias 1982, Sáiz & Carvajal 1990), e información sobre el género *Dorymyrmex* también en cuatro artículos (Ipinza 1971b, Snelling 1975, Ipinza-Regla & Covarrubias 1989, Sáiz & Carvajal 1990).

Finalmente, existen antecedentes biológicos en tres publicaciones para el género *Myrmelachista* (Ipinza 1971b, Ipinza-Regla 1985, Solervicens et al. 1991), datos en un par de trabajos para los géneros *Antichthonidris* (Snelling 1975, Ipinza-Regla & Covarrubias 1982), *Heteroponera* (Ipinza & Capurro 1972, Ipinza & Schenone 1972), *Pseudomyrmex* (Sáiz & Carvajal 1990, Solervicens et al. 1991), y *Tetramorium** (Ipinza-Regla & Covarrubias 1982, Ipinza-Regla 1985); y alguna información traza presente en un artículo para los géneros *Lasiophanes* (Solervicens et al. 1991), *Monomorium** (Ipinza-Regla & Covarrubias 1982), y *Pheidole* (Ipinza-Regla & Covarrubias 1982).

DISCUSIÓN

Durante los primeros tres períodos del siglo XX (1900-1929) la información existente respecto a hormigas estuvo basada principalmente en el reporte de pequeñas notas sobre la vida de hormigas foráneas. La Revista Chilena de Historia Natural fue el principal órgano de difusión de este tipo de información, lo cual fue promovido esencialmente a través de su editor C. Porter, el cual tendría además una fuerte injerencia en el impulso y desarrollo de la ciencia y entomología en Chile (González 1983, Etcheverry 1992). A pesar de los avances conseguidos durante estos años en el cultivo de las ciencias naturales (González 1983), la nula productividad nacional respecto a la temática aquí tratada puede haber estado ligada a una visión de época en que "*la ciencia sólo se adquiere a través del discurso o los libros*" y/o la existencia de "*una reverenciosa sumisión ante la abrumadora presencia de la capacidad creadora de la ciencia europea, unida a una pesimista apreciación del vuelo intelectual o inventivo de los chilenos*" (Croxatto 1982). Otra razón que ha sido sugerida como causa de esta baja producción en las ciencias naturales, son las restricciones presupuestarias y una reducción de la planta de investigadores que afectó al Museo Nacional de Historia Natural durante esta época (Veloso 1982).

En la década del 30' se produce un importante auge en la generación de información sobre hormigas chilenas, lo cual esta ligado esencialmente al nombre de W. Goetsch, el cual elaboró en solitario y en coautoría con C. Menozzi catálogos y listas de especies de los formícidos presentes en Chile. Además, este investigador desarrolló una serie de experimentos destacados e ingeniosos para su época, en los cuáles analizaba el rol de la comunicación química sobre las conductas de movimientos exhibidas por obreras entre el nido y una fuente de alimento, aspectos que están plenamente vigentes en líneas de investigación desarrolladas en la actualidad (Holldobler & Wilson 1990). Posteriormente, las décadas del 40' y 50' son percibidas como un período de nula productividad en la temática tratada, lo cual puede haber estado determinado por el cese de C. Porter en sus funciones de editor de la Revista Chilena de Historia Natural en 1940 y su posterior fallecimiento en 1942 (González 1983), lo cual habría tenido un profundo impacto en el auge que venía experimentando la entomología en el país. A esto hay que agregar, que hasta fines de los años 40' el cultivo de las ciencias naturales en Chile seguía siendo de orden clásico, es decir, una disciplina descriptiva y comparativa, mientras que a nivel mundial lo que imperaba era la formación de científicos especializados en investigar las distintas disciplinas en que se subdividían las ciencias naturales; todo lo cual generaba el siguiente escenario "*existía en Chile un período de suspenso en cuanto al rumbo a seguir y los museos se preocupaban más de conservar que de investigar*" (González 1983).

A partir de la década de los 60' se produce una revitalización de la producción científica en el tema tratado, lo cual parece estar ligado a una canalización de la enseñanza e investigación de las ciencias naturales en el ambiente de la universidad. Específicamente las actividades desarrolladas por J. Herrera en el Centro de Estudios Entomológicos, G. Mann en el Centro de Investigaciones Zoológicas, y la creación por parte de J. Gómez Millas de la Facultad de Ciencias de la Universidad de Chile, dieron un fuerte impulso al cultivo de disciplinas como la zoología y ecología (Croxatto 1982, Hajek 1982, Veloso 1982, González 1983). Durante la década del 70' la elaboración de la tesis doctoral de J.H. Hunt (1973) - inmersa en un estudio de convergencia ecológica entre ecosistemas mediterráneos de Chile y California, dependiente del "International Biological Program" (IBP) - constituyè un hito destacado en el que se analiza y compara la ecología de comunidades de hormigas en estas regiones, recopilándose información básica sobre la biología de varias especies de formícidos. La importancia de este tipo de información alcanza su máxima expresión con la publicación del valioso catálogo acerca de las hormigas de Chile por parte de Snelling & Hunt (1975), el cual es utilizado en la actualidad para la identificación y determinación de organismos obreras a nivel de subfamilias, géneros y especies. Paralelamente, durante estos años aparecen textos clásicos (Wilson 1971, Oster & Wilson 1978) que incentivarán y fomentarán a nivel nacional el estudio biológico de estos insectos sociales.

En la década de los 80', sobresalen los trabajos de Ipinza-Regla y colaboradores, los cuáles se concentran en estudiar especies del género *Camponotus* abordando una serie de temáticas ecológicas. La aparición continuada de la Revista Chilena de

Entomología y la edición de una nueva revista - Acta Entomológica Chilena - durante estos años, juegan un papel primordial en la divulgación de esta información. A pesar que el año 1983 se comienza a reeditar la Revista Chilena de Historia Natural, la aparición de información sobre hormigas chilenas ha sido prácticamente nula en esta publicación. En el libro "Introducción a los insectos de Chile" de Peña (1986) se hace una breve mención de dos páginas a las hormigas chilenas que presentan un amplio rango de distribución y resultan ser más comunes y/o abundantes; por otra parte, en la segunda edición en lengua castellana de la obra "La vida social de las hormigas" de Goetsch (1987) se documentan varios aspectos acerca de la biología de hormigas chilenas; adicionalmente, en otro texto (González 1989) se menciona la importancia económica de la "hormiga argentina" (*Linepithema humile**) como plaga primaria. Finalmente, durante la década de los 90' se continúan y mejoran los aspectos desarrollados durante los años 80'; es así como a la producción continuada de Ipinza-Regla, se suman y destacan los trabajos de Medel y colaboradores sobre aspectos comunitarios de ensambles de hormigas granívoras. Además, durante este período en una serie de libros se entregan antecedentes acerca de las especies de hormigas que constituyen plagas secundarias (Prado1991) y/o presentan algún interés económico (Artigas 1994), el estado del conocimiento de los formícidos chilenos (Rojas & Elgueta 1995), y el daño producido por ciertas especies en cítricos (Ripa & Rodriguez 1999). Por último, es importante mencionar que a comienzos de esta década se publicó por parte de Holldobler & Wilson (1990) la monumental obra "The ants" – texto de consulta obligada para cualquier interesado en el tema - en la cual existe alguna información traza sobre Chile y sus hormigas.

En relación a las principales temáticas estudiadas, se puede afirmar que a partir de la década del 20' los trabajos sobre taxonomía fueron preponderantes y tuvieron una aparición periódica (salvo durante la década del 40'), culminando con la publicación del trabajo de Snelling & Hunt (1975). Este fenómeno puede deberse a que cuando se comienza el estudio de un taxón, un primer e importante paso es conocer cuántas y qué tipo de especies existen. Sin embargo, en los últimos 25 años no se han publicado trabajos taxonómicos en hormigas chilenas, lo cual esta asociado a un patrón general de disminución de especialistas interesados en trabajar actualmente en esta temática (Simonetti 1995). De hecho, en Chile existen sólo cinco entomólogos nacionales que trabajan en forma regular en aspectos taxonómicos de Hymenoptera (Solervicens 1995), de los cuáles sólo uno (J. Ipinza-Regla) se especializa en Formicidae (Solervicens, comunicación personal). Un segundo y necesario paso en el estudio de un taxón, consiste en analizar aspectos básicos de la biología de los organismos; lo cual se corresponde con lo sucedido durante la década del 80' y 90', donde han tenido una fuerte preponderancia artículos sobre la ecología (e.g. uso del hábitat, períodos de actividad, conductas tróficas) de las hormigas chilenas (e.g. trabajos de Ipinza-Regla, Medel y colaboradores).

Respecto a los géneros de formícidos que han concentrado el interés de las investigaciones, no constituye un hecho sorprendente que los estudios se hayan focalizado principalmente en *Camponotus* y *Solenopsis*, debido a que estos géneros corresponden a hormigas que poseen un amplio rango de distribución y se presentan en forma común y abundante en el país (Snelling & Hunt 1975, Peña 1986, Artigas 1994). Por otra parte, destacan los trabajos que se han centrado en géneros de hormigas granívoras (*Conomyrma*, *Brachymyrmex*, *Pogonomyrmex*), así como información reciente referida a los efectos y consecuencias como plaga que tendría la especie *Linepithema humile** (González 1989, Prado 1991, Artigas 1994, Ripa & Rodriguez 1999). Algunas características conspicuas de estas especies como su tamaño corporal, coloración, tipo de nido, nivel de actividad, forma de movimiento, y conducta de alimentación, sumado al hecho de su presencia en Chile central (donde se ha concentrado la investigación), las convierten en objetos preferidos de estudio.

Es posible que existan datos marginales sobre biología de hormigas chilenas en otros artículos; sin embargo, los antecedentes aquí revisados corresponden a los trabajos más representativos y que de alguna forma dan cuenta del estado del conocimiento de este grupo de organismos. Se espera que esta información pueda contribuir a biólogos interesados en estudiar a las hormigas y su vida social, así como ayude a fomentar la publicación de datos y tesis de investigadores que han trabajado en el tema. Algunas carencias generales que han sido detectadas en el conocimiento de los insectos de Chile, se proyectan en el estudio de estos organismos. Es así como se hace necesario fomentar la formación de taxónomos y sistemáticos especializados en este grupo, complementar y enriquecer las colecciones taxonómicas, incentivar su estudio no sólo en localidades de Chile central sino también en regiones del norte y sur del país (i.e. análisis biogeográficos), y acceder a información básica referente a los ciclos de vida y ecología de estos organismos (Solervicens 1995). El énfasis de estas tareas debiera ser puesto en las hormigas endémicas, debido a su importancia e implicancia en problemas de biodiversidad y conservación de especies. Las hormigas chilenas constituyen un excelente modelo de estudio para desarrollar varias líneas de investigación. En el ámbito de la ecología conductual de individuos, sería posible la complementación de cuerpos de conocimiento tan diversos como: forrajeo social o en grupo, navegación espacial, uso de información, y comunicación química entre obreras. Los análisis de proporción de sexos y castas, sobrevivencia y reproducción de nidos, estructura y variabilidad genética de las colonias, permitirían abordar problemáticas de la biología de poblaciones. El estudio de las interacciones entre especies de hormigas y con otros insectos y plantas, así como la partición del hábitat y de la actividad temporal por parte de formícidos, incrementaría la comprensión de la estructura comunitaria de los ensambles de hormigas. Finalmente, el análisis de la remoción y mezcla de sustrato por parte de la fauna mirmecológica, permitiría determinar su rol e impacto en funciones y procesos ecosistémicos. La recopilación de toda esta información posibilitaría abordar preguntas como ¿existen diferentes y complejas estrategias adaptativas cuando obreras y/o colonias se ven confrontadas a ambientes espacial y temporalmente variables?, y evaluar sus implicancias en el ámbito de la ecología y biología evolutiva de insectos sociales.

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LEYENDA DE FIGURAS

Figura 1: Dinámica temporal de la producción de publicaciones sobre formícidos chilenos durante el siglo XX. La barra blanca corresponde a información sobre hormigas foráneas divulgada en revistas científicas nacionales, y la barra oscura a antecedentes sobre especies presentes en Chile publicados tanto en revistas nacionales como extranjeras; la suma de ambas barras representa el total de publicaciones por década.

Figura 2: Principales temáticas de estudio sobre hormigas chilenas, aparecidas en publicaciones nacionales y extranjeras durante el período 1900-1999.

Figura 3: Géneros de hormigas chilenas en los cuáles se ha concentrado la investigación durante los últimos cien años. El * corresponde a género cuyas especies son introducidas.

Figura 1

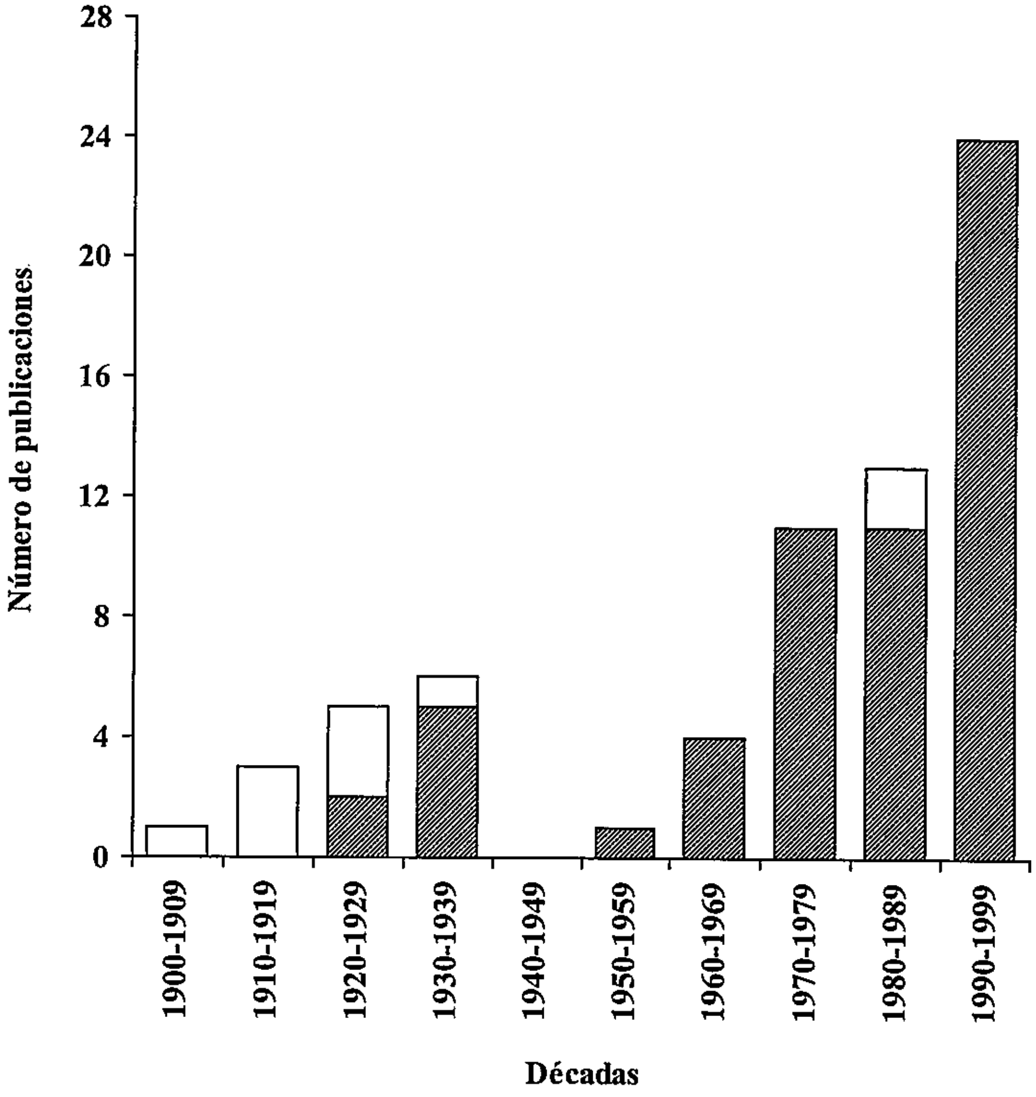
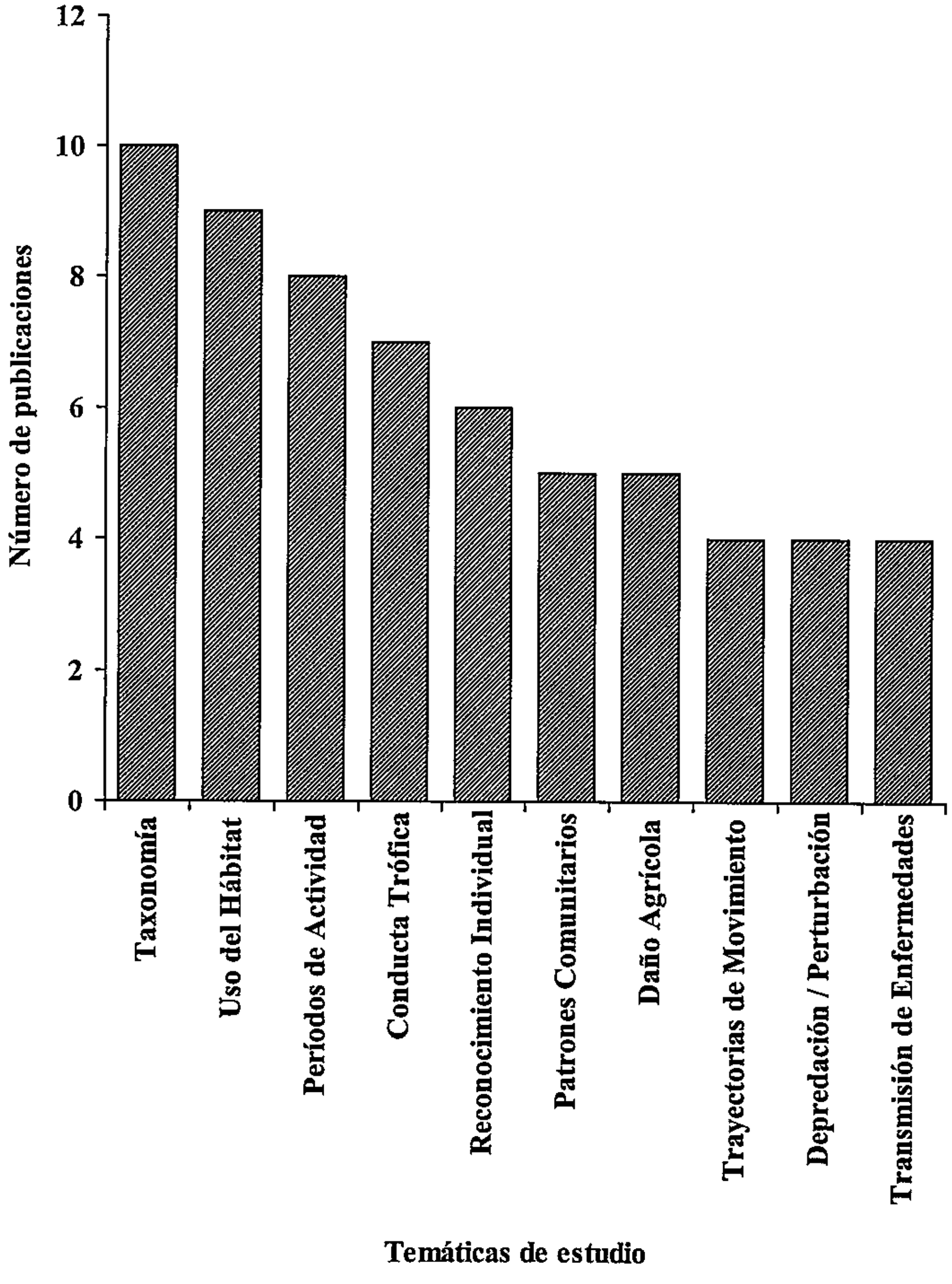

28
24
20
16
12
8
4
0
Número de publicaciones
1900-1909
1910-1919
1920-1929
1930-1939
1940-1949
1950-1959
1960-1969
1970-1979
1980-1989
1990-1999
Décadas

Figura 2


12
10
8
6
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2
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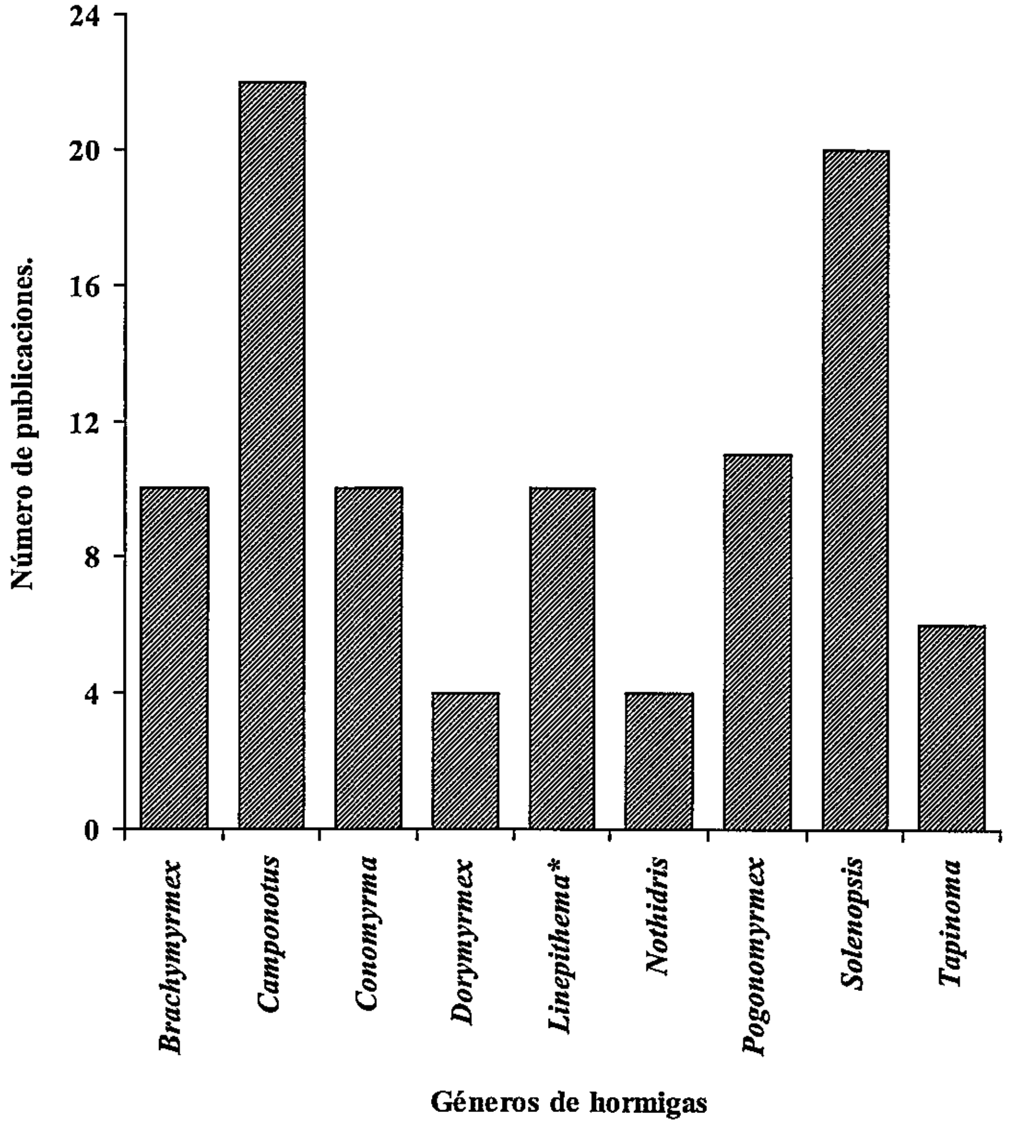
Número de publicaciones
Taxonomía
Uso del Hábitat
Períodos de Actividad
Conducta Trófica
Reconocimiento Individual
Patrones Comunitarios
Daño Agrícola
Trayectorias de Movimiento
Depredación / Perturbación
Transmisión de Enfermedades
Temáticas de estudio

Figura 3



24
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Número de publicaciones.
Brachymyrmex
Camponotus
Conomyrma
Dorymyrmex
*Linepithema**
Nothidris
Pogonomyrmex
Solenopsis
Tapinoma
Géneros de hormigas

Tabla 1. Principales trabajos sobre biología de hormigas chilenas. Para cada artículo se detalla la línea de investigación analizada, los géneros de hormigas estudiados, y un comentario sobre su contenido. Se excluyen seis trabajos sobre taxonomía que corresponden a listas y/o catálogos de especies (Goetsch 1933, Kusnezov 1959, 1962, Kempf 1970, 1972, Snelling & Hunt 1975). Los símbolos corresponden a especies: *= introducidas, ^{N}= con distribución neotropical, ^{P}= con distribución patagónica, ^{E}= endémicas.

Referencia(s)	**Temática(s) estudiada(s)**	**Especie(s) analizada(s)**	**Observaciones**
Cekalovic (1964)	Taxonomía	*Pogonomyrmex vermiculatus*^{P}	Se documenta la presencia de esta especie en la región de Magallanes
Córdova-Yamauchi et al. (1998)	Comunicación química	*Linepithema humile**	Se evaluó la conducta de "atención" de áfidos por parte de esta especie, cuando es expuesta a compuestos volátiles (semioquímicos) involucrados en la conducta de espaciamiento de estos áfidos
Covarrubias et al. (1987)	Uso del hábitat	*Camponotus chilensis*^{P}, *C. hellmichi*^{E}, *C. morosus*^{E}, *Brachymyrmex giardii*^{E}, *Pogonomyrmex odoratus*^{P}, *Solenopsis latastei*^{N}, *S. germaini*^{E}, *Conomyrma pogonius*^{E}, *C. antarcticus*^{P}	Se establecen correlaciones entre gradiente altitudinal, cobertura vegetal, pH suelo, y número de especies, número de nidos de hormigas
Eaton & Medel (1994)	Genética de colonias	*Camponotus chilensis*^{P}	Se infiere la estructura reproductiva (fundación monogínica y/o poligínica

			del nido) y el grado de parentesco en obreras de diferentes colonias
Ettershank (1965)	Taxonomía	*Nothidris bicolor*^{E}	Se realiza el diagnóstico de esta especie en la región de Coquimbo
Fuentes & Ipinza (1979)	Depredación, Perturbación	*Camponotus chilensis*^{P}, *C. morosus*^{E}, *C. hellmichi*^{E}, *C. ovaticeps*^{E}	Se analiza la presencia de formicídos en el contenido estomacal de *Liolaemus monticola* (Reptilia)
Fuentes et al. (1996)	Períodos de actividad, conductas tróficas, patrones comunitarios	*Solenopsis gayi*^{E}, *Conomyrma goetschi*^{E}, *Brachymyrmex giardii*^{E}	En localidades de la región árida y semiárida de Chile, se analizan: actividad de hormigas en el rango diario de temperaturas del suelo, sobreposición en utilización de cebos, y correlaciones entre precipitaciones y abundancias relativas de las especies
Goetsch (1930a, 1930b)	Trayectorias de movimiento	*Solenopsis gayi*^{E}, *Pogonomyrmex bispinosus*^{E}	Se estudian las conductas de exploración y orientación de los movimientos exhibidos por obreras entre el nido y una fuente de alimento
Grez et al. (1986)	Conductas tróficas	*Camponotus morosus*^{E}	Se estudia la dieta de esta especie en el matorral de Chile central durante la estación de verano
Hunt (1974)	Períodos de actividad	*Conomyrma antarcticus*^{P}, *Tapinoma antarcticum*^{E}	Se analiza el efecto de la temperatura superficial del suelo sobre las actividades de forrajeo, y la coexistencia de estas especies
Ipinza-Regla (1969, 1971a)	Períodos de actividad	*Solenopsis gayi*^{E}, y formícidos en general	Se analiza el efecto de la temperatura y humedad relativa, sobre la

			abundancia y período de actividad de las hormigas
Ipinza-Regla (1971b)	Uso del hábitat	*Linepithema**, *Dorymyrmex*^{E}, *Tapinoma*^{E}, *Solenopsis*, *Pogonomyrmex*, *Brachymyrmex*^{E}, *Myrmelachista*, *Camponotus*	Se documenta la abundancia de la fauna mirmecológica en el estrato árboreo-arbustivo de la sabana espinosa central (Curacaví, V región)
Ipinza-Regla (1985)	Depredación, Perturbación	*Camponotus morosus*^{E}, *C. chilensis*^{P}, *Brachymyrmex giardii*^{E}, *Myrmelachista hoffmanni*^{E}, *Pogomoyrmex bispinosus*^{E}, *P. angustus*^{P}, *Tetramorium caespitum**, *Linepithema humile**	Se determina la presencia de formícidos en el contenido gástrico de *Liolaemus monticola* (Reptilia)
Ipinza & Capurro (1972), Ipinza & Schenone (1972)	Transmisión de enfermedades	*Heteroponera carinifrons*^{E}	Se documentan cuadros anafilácticos en la región de Antofagasta provocados por la "picadura" de esta especie
Ipinza-Regla & Covarrubias (1982)	Uso del hábitat	*Solenopsis gayi*^{E}, *S. latastei*^{N}, *S. germaini*^{E}, *S. helena*^{E}, *S. dysderces*^{E}, *S. patagonica*^{P}, *Pogonomyrmex vermiculatus*^{P}, *P. bispinosus*^{E}, *P. angustus*^{P}, *P. odoratus*^{P}, *P. laevigatus*^{P}, *Nothidris latastei*^{E}, *N. bicolor*^{E}, *N. cekalovici*^{E}, *Antichthonidris*	Se analiza la distribución de estas especies (subfamilia Myrmicinae), en relación al tipo de hábitat y condición bioclimática que utilizan

		denticulatus^{P}, _A. bidentatus_^{P}, _Tetramorium guineense_*, _T. caespitum_*, _Pheidole chilensis_^{N}, _Monomorium floricola_*	
Ipinza-Regla & Covarrubias (1989)	Uso del hábitat	_Conomyrma antarcticus_^{P}, _C. chilensis_^{E}, _C. goetschi_^{E}, _C. hunti_^{E}, _C. hypocritus_^{E}, _C. incomptus_^{E}, _C. minutus_^{P}, _C. pappodes_^{E}, _C. pogonius_^{E}, _C. tener_^{P}, _Dorymyrmex agallardoi_^{E}, _Linepithema humile_*, _L. oblonga_*, _Tapinoma antarcticum_^{E}	Se analiza la distribución de estas especies (subfamilia Dolichoderinae) de acuerdo a su presencia en diferentes regiones bioclimáticas
Ipinza-Regla & Morales (1998)	Reconocimiento entre individuos	_Camponotus morosus_^{E}	Se compara el nivel de reconocimiento entre obreras pertenecientes a colonias artificiales (laboratorio) y naturales (terreno)
Ipinza-Regla et al. (1981)	Transmisión de enfermedades	_Linepithema humile_*	Se documenta el potencial efecto de esta especie como vector intrahospitalario de bacterias mesófilas
Ipinza-Regla et al. (1983)	Uso del hábitat	_Camponotus chilensis_^{P}, _C. hellmichi_^{E}, _C. morosus_^{E}, _Brachymyrmex giardii_^{E}, _Pogonomyrmex odoratus_^{P}, _Solenopsis latastei_^{N}, _S. germaini_^{E},	En un gradiente altitudinal del sector precordillerano de Chile central, se estudia la abundancia y distribución espacial de especies y nidos de hormigas

		Conomyrma pogonius^{E}, *C. antarcticus*^{P}	
Ipinza-Regla et al. (1984)	Transmisión de enfermedades	*Linepithema humile**	Se documenta el potencial efecto de esta especie como vector de microorganismos enteropatógenos en industrias de alimentos
Ipinza-Regla et al. (1986)	Uso del hábitat	*Camponotus morosus*^{E}	En un sector precordillerano de Chile central, se estudia la distribución espacial de nidos de esta especie
Ipinza-Regla et al. (1988)	Períodos de actividad	*Camponotus morosus*^{E}	En una localidad precordillerana de Chile central, se estudia la actividad diaria de obreras exploradoras, durante las estaciones de primavera y verano
Ipinza-Regla et al. (1990)	Uso del hábitat	*Brachymyrmex giardii*^{E}, *Camponotus morosus*^{E}, *Solenopsis gayi*^{E}, *Conomyrma hypocritus*^{E}	En un área precordillerana de Chile central, se analiza la distribución espacial, asociación interespecífica y asociación con arbustos, de los nidos de estas especies
Ipinza-Regla et al. (1991)	Reconocimiento entre individuos	*Camponotus morosus*^{E}	Se estudia el reconocimiento entre individuos conespecíficos, en nidos artificiales
Ipinza-Regla et al. (1992)	Nota técnica	*Camponotus morosus*^{E}	Se analiza una técnica de revelado fotográfico para marcaje de individuos
Ipinza-Regla et al. (1993a)	Trayectorias de movimiento	*Camponotus morosus*^{E}	En un área precordillerana de Chile central, se determinan la distancia recorrida, forma de movimiento y ámbito de

			hogar de esta especie
Ipinza-Regla et al. (1993b)	Reconocimiento entre individuos	*Camponotus morosus*^{E}	Se estudia el efecto de la distancia geográfica entre colonias sobre la conducta de reconocimiento entre obreras de esta especie
Ipinza-Regla et al. (1994)	Reconocimiento entre individuos	*Camponotus morosus*^{E}, *Brachymyrmex giardii*^{E}	Se analiza el nivel de "hermetismo" presente en las conductas de reconocimiento entre individuos homo y hetero específicos
Ipinza-Regla et al. (1996)	Reconocimiento entre individuos	*Camponotus morosus*^{E}, *C. chilensis*^{P}, *Solenopsis gayi*^{E}	Se determina la influencia de la distancia filogenética sobre las conductas de reconocimiento entre los individuos de estas especies
Ipinza-Regla et al. (1998)	Reconocimiento entre indivduos	*Camponotus morosus*^{E}	Se analiza en terreno la conducta "hermetica" de nidos de esta especie, frente a individuos intrusos homoespecíficos dispuestos a diferentes distancias de la entrada del nido
Larraín et al. (1995)	Daño agrícola	*Solenopsis gayi*^{E}	Se documenta el daño producido por esta especie, a árboles nuevos de mandarinos y plantas de pepino dulce
Lewis & Peredo (1993)	Uso del hábitat	*Camponotus morosus*^{E}	Se documenta la presencia de esta especie en galerías abandonadas del "taladrador de la madera" (Lepidoptera) en bosques de raulí
Medel & Vásquez (1994)	Períodos de actividad, conductas	*Conomyrma goetschi*^{E}, *Brachymyrmex giardii*^{E}, *Solenopsis*	Estudio comparativo entre ensambles de hormigas granívoras presentes en

	tróficas, patrones comunitarios	*gayi*^{E}	zonas áridas de Chile y desierto del Monte en Argentina, donde se analizan: actividad de hormigas en el rango diario de temperaturas del suelo, distancia y tipo de forrajeo (individual o columnar)
Medel (1995)	Conductas tróficas, patrones comunitarios	*Conomyrma goetschi*^{E}, *Brachymyrmex giardii*^{E}, *Solenopsis gayi*^{E}	Se examina el efecto de procesos históricos y de convergencia, sobre los patrones ecológicos de ensambles de hormigas granívoras presentes en Australia, Norte América y Sur América; se analizan factores como: abundancia de hormigas en cebos, distancia y tipo de forrajeo
Medel & Fuentes (1995)	Períodos de actividad, conductas tróficas, patrones comunitarios, trayectorias de movimiento	*Pogonomyrmex vermiculatus*^{P}, *Solenopsis gayi*^{E}	En una localidad semiárida del norte de Chile, se documenta la actividad y forma de movimiento individual, dieta, y abundancia poblacional de estas especies
Moroni (1977)	Depredación, Perturbación	*Solenopsis gayi*^{E}	Se documenta la presencia de esta hormiga en estómagos de *Pitius pitius* (Ave)
Porter (1923b)	Taxonomía	*Solenopsis gayi*^{E}, *S. patagonica*^{P}, *Tapinoma antarcticum*^{E}	Se documenta el diagnóstico de estas especies efectuado por parte de Santschi
Ríos-Aramayo & Jiménez (2000)	Períodos de actividad, conductas tróficas	*Camponotus hellmichi*^{E}	Se estudia el número de visitas y la conducta de alimentación de estas hormigas, en cactus (*Echinopsis chilensis*) sin infestación e infestados por

			muérdagos (*Tristerix aphyllus*) y/o conchuelas (*Saissetia oleae*)
Ripa (1987)	Daño agrícola	*Linepithema humile**	Se discute el efecto protector de esta hormiga hacia insectos plagas (pulgones, conchuelas, chanchitos y mosquitas blancas) de árboles frutales
Ripa et al. (1993a)	Daño agrícola	*Linepithema humile**	Se evalua la acción de diferentes tratamientos con insecticidas para controlar la “hormiga argentina”, lo cual permite el manejo del “chanchito blanco” en cultivos de vid
Ripa et al. (1993b)	Daño agrícola	*Linepithema humile**	Se analizan distintas técnicas de exclusión de esta especie a cítricos, y de esta forma el manejo de insectos plagas
Ripa et al. (1998)	Daño agrícola	*Linepithema humile**, *Solenopsis gayi*^{E}	Se revisa los daños directos e indirectos producidos por estas especies a la agricultura, y se discute la eficiencia de diferentes métodos de control de estas hormigas
Saiz & Carvajal (1990)	Depredación, Perturbación	*Solenopsis gayi*^{E}, *Nothidris latastei*^{E}, *Pogonomyrmex bispinosus*^{E}, *P. angustus*^{P}, *Pseudomyrmex lynceus*^{E}, *Tapinoma antarcticum*^{E}, *Dorymyrmex sp.* ^{E}, *Camponotus distinguendus*^{P}	En el sector de Ocoa (V región), se evalúa el efecto inmediato – y durante los dos años siguientes - de una perturbación de fuego, sobre la abundancia poblacional y capacidad de recuperación de estos formícidos

Snelling (1975)	Taxonomía	*Nothidris cekalovici*^{E}, *Solenopsis dysderces*^{E}, *Dorymyrmex agallardoi*^{E}, *Conomyrma hunti*^{E}, *C. hypocritus*^{E}, *C. incomptus*^{E}, *C. pappodes*^{E}, *C. pogonius*^{E}	Se documenta la descripción de estas nuevas especies
Solervicens et al. (1991)	Uso del hábitat	*Camponotus morosus*^{E}, *C. ovaticeps*^{E}, *Pogonomyrmex odoratus*^{P}, *P. angustus*^{P}, *Pseudomyrmex lynceus*^{E}, *Conomyrma chilensis*^{E}, *Brachymyrmex laevis*^{E}, *Lasiophanes valdiviensis*^{E}, *Myrmelachista hoffmanii*^{E}, *Solenopsis gayi*^{E}, *Tapinoma antarcticum*^{E}	Durante la estación de primavera y en laderas de exposición norte y sur, se estudia la entomofauna de follaje y de superficie de suelo en la Reserva Río Clarillo (región Metropolitana)
Vásquez et al. 1995	Patrones comunitarios	Formícidos en general	En el matorral de Chile central y durante cuatro estaciones, se estudia la intensidad de granivoría en hábitats abiertos y cerrados en vegetación