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Distance and Patch Richness Affect the Use of Exploitation
versus Interference Competition in Central Place Foraging
Eastern Chipmunks, Tamias striatus

Luc Bouisset

A Thesis
in
The Department
of
Biology

Presented in Partial Fulfillment of the Requirements
for the Degree of Master of Science at
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ABSTRACT

Distance and Patch Richness Affect the Use of Exploitation
versus Interference Competition in Central Place Foraging
Eastern Chipmunks, Tamias striatus

Luc Bouisset

When central place foragers compete for food patches, they should interfere with each other less and be tolerant of one another more as distance between the patch and the central place and/or patch richness increase(s). To test these social central place foraging model's predictions of a gradual transition from interference to exploitation competition, experiments were conducted in the field on ten dyads of eastern chipmunks (Tamias striatus), contesting access to experimental food patches that were placed at various distances from burrows and differed in seed density. On the one hand, chipmunks tolerated each other less from short to intermediate distance, and more from intermediate to longest distance. On the other hand, the richer the patch, the more likely were chipmunks to tolerate one another. The model predicted the effect of patch richness on the competing behaviours of central place foragers in contests over food patches, but not the effect of distance.

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I INTRODUCTION

How animals respond to competition for resources is a major determinant of their social systems. For example, group foraging may require that individuals mostly compete by scramble strategies. Similarly, the aggressive defence of resources (contest strategies) may lead to the evolution of a wide range of social systems from territoriality to systems based on dominance hierarchies (Lott 1991). Thus, social systems may often be pictured as the consequences of the choice of competitive strategies by animals.

The eastern chipmunk (Sciuridae: Tamias striatus) is a small (~100 g), diurnal, forest-dwelling rodent, which feeds on seeds forming patches under the crown of producing trees. Seeds are carried in specialized cheek pouches to an underground burrow, in which they are hoarded for later consumption (Allen 1938; Elliott 1978). Burrows are centrally located in relatively circular and symmetrical home ranges of about 0.2 - 0.4 ha (Elliott 1978). The home range's use-intensity per unit area is greatest within a core area with a radius of about 12 m, and least at the peripheries (Elliott 1978; Getty 1981b). The chipmunk defends the core area by chasing intruders from it, and rarely tolerates a conspecific at close distance throughout most or all of the home range (Elliott 1978; Yahner 1978; Getty 1981a, b). However, despite this important investment in aggressive defence behaviour,

chipmunks actually do not attain exclusive use of a foraging area. Overlap between neighbour's home ranges is extensive ($\geq 50\%$), and social interactions between chipmunks -such as contests over food patches- are frequent (Elliott 1978; Getty 1981a).

The chipmunk's social system conforms more closely to the establishment of dominions (zones of dominance), rather than exclusive territories (Wittenberger 1981). Unlike classic territoriality, dominions allow for a certain flexibility in the social encounters. Thus, occasionally several chipmunks may be observed feeding together in a small area (Elliott 1978; L.-A. Giraldeau, D.L. Kramer & H. Lair pers. com.; pers. obs.). Elliott (1978, p. 37), for instance, "(...) observed as many as seven individuals foraging under the (crown of a single) tree at one time, these chipmunks commonly passing within several feet of one another without arousing any overt aggressive behavior." Elliott (1978) noticed that the tree, a red maple (Acer rubrum), had produced an abundant seed crop, and was situated at a long distance (> 25 m) from any individual's burrow. The question arises then: how can distance and food abundance permit several chipmunks to forage together on the same patch, instead of chasing each other?

Answers to such a question concern the broad research area of competition for resources, or resource defence

(Milinski & Parker 1991). Food, mates, shelters, mating place, breeding space, or any other requirement which tends to maximize an animal's fitness -i.e. its survival and reproduction- are resources. Competition occurs when any of these resources is potentially limited in availability with regard to the number of individuals which use it, and is often but not always expressed through intra/interspecific aggressiveness (Krebs & Davies 1987; Keddy 1989). When animals compete for resources, they make two sets of decisions: the first is whether a particular resource is worth competing for, and if so, the second is what competition strategy(ies) is(are) to be used in a contest with a particular opponent over that resource (Archer 1988). Separate research approaches have been developed to deal with each of these decisions, and I will briefly review each in turn.

I.1 Territoriality

When are resources worth competing for? To answer this question, Brown (1964) first applied notions of the theory of economics to resource defence, by introducing the concept of economic defendability of a resource. For a given set of circumstances, whether a resource is defended depends on the balance between the benefits obtained and the costs of defence. Benefits to individuals may include an exclusive

access to or use of a food source, exclusive mating rights, a safe breeding space, etc, whereas costs may include time and energy spent in defence, risks of injury from fighting, etc. Assuming that an animal is designed through natural selection to behave so as to maximize its fitness, resource defence should evolve whenever the benefits exceed the costs; maximum fitness is attained when the positive difference between the benefits and the costs is maximized (the optimal balance).

Two main factors influence the economic defendability of a resource: (1) the resource quality and its spatio-temporal distribution in the environment; and (2) the number of competitors (intruder pressure) and the extent of individual differences in competitive ability (Davies & Houston 1984). Brown's (1964) concept has been used to develop economic (optimality) models that predict the occurrence of resource defence, as well as the optimal amount of resource for an animal to defend. Up to now, these models and the studies designed to test their predictions, have traditionally focused on feeding territoriality, particularly in nectarivorous birds (Gill & Wolf 1975; Carpenter & MacMillen 1976; Armstrong 1991; Marchesseault & Ewald 1991), but also in other taxa (Myers & al. 1981; Stimson Wilcox & Ruckdeschel 1982; Wyman & Hotaling 1988). Furthermore, recent experimental work investigated the effect of spatial and temporal clumping of food in fishes (Grant & Kramer 1992;

Bryant 1993; Grand & Grant 1994; Grant & Guha 1993).

I.ii Competitive Strategies

The second research approach deals with the following question: given that resources are economically defensible, which competition strategies ought to be used by contestants? To answer this question, Maynard Smith & Price (1973) first applied notions of the theory of games to resource defence. By doing so, resource defence can be studied not primarily as a relationship between an animal and a resource in the environment -as in the case for economic models- but also as a form of social behaviour (Archer 1988). In contests over resources, the way for an individual to fight depends on what others are doing. Animal conflict behaviour therefore can be modeled as a game in which players use different strategies; the resulting benefits and costs of each depends on the behaviour of competitors, i.e. on which other strategies are encountered (the available alternatives), and how often (their frequencies) (Maynard Smith 1982).

Theoretically, the aim of game theory models is to determine the Evolutionarily Stable Strategy (ESS) of a population for a given set of circumstances. An ESS is a strategy which can not be outcompeted by any other available alternatives; it is therefore the optimal strategy insofar as it is better suited to current conditions than is any other

strategy defined in the model used (Maynard Smith 1982). Practically, game theory models have been mostly used to predict -at an individual rather than at a population level- the optimal strategies in dyadic contests for a given set of conditions, as well as the outcome of such interactions (i.e. who is to be the winner gaining an exclusive access to the contested resource) (Maynard Smith 1982).

Early game theory models assumed symmetric contests; opponents were equal in all respects. However, most real animal conflicts involve competitors who are dissimilar to one another in at least one aspect. Accordingly, more recent models consider asymmetric contests. They predict that dominance results from asymmetries between contestants. These asymmetries are of 3 types (Maynard Smith & Parker 1976; Hammerstein 1981; Maynard Smith 1982): (1) fighting ability or Resource Holding Potential (RHP) asymmetry: one competitor may be better able to fight and defend a resource than another; (2) resource value or payoff asymmetry: one competitor may value a resource more highly than another; and (3) uncorrelated asymmetry: an asymmetry that is not related to either RHP or value, as one competitor may 'own' a resource and another may not.

Up to now, studies relevant to the game theory approach to resource defence have investigated principally how asymmetries are used to settle contests over territories

(Ewald 1985; Beaugrand & al. 1991; Rosenberg & Enquist 1991; Sandell & Smith 1991), mates (Faber & Baylis 1993) or food patches (Hansen 1986; Silbaugh & Ewald 1987).

I.iii An Integration of the Two Approaches to Chipmunk Social Foraging

Any attempt to explain the strategies of chipmunks contesting a resource patch necessitates a comprehension of the economics underlying their foraging behaviour. Chipmunks are Central Place Foragers (CPFs), animals which "do not consume their prey where they are captured but return with them to some fixed central place where they are eaten, stored, or fed to dependent offspring" (Orians & Pearson 1979, p.156). Other examples are insects (Hölldobler & Lumsden 1980; Kasuya 1982; Kacelnik & al. 1986), altricial birds which are feeding their young (Carlson & Moreno 1982; Krebs & Avery 1985; Kacelnik & Cuthill 1990; Kaspari 1991), and hoarding mammals (Fryxell & Doucet 1991).

In an extension to optimal foraging theory, Orians & Pearson (1979) showed how CPFs should select prey, patches, and load sizes to maximize their Rate of Food Delivery (RFD) to the central place. All these foraging decisions are affected by the distance between the patch and the central place, and patch quality. Studies on the eastern chipmunk's foraging behaviour have provided consistent qualitative

support for several predictions of the central place foraging model (Kramer & Nowell 1980; Giraldeau & Kramer 1982; Kramer & Weary 1991; Bowers & Ellis 1993; Giraldeau & al. in press; Lair & al. in press).

Ydenberg & al. (1986) proposed that competition for resources in CPFs can be modeled by modifying Orians & Pearson's (1979) model to include the consequences of conflict over food. They hypothesized that interference behaviour at a patch can be used by one forager to reduce a competitor's RFD, and hence influence its patch exploitation decision. The Ydenberg & al. (1986) model predicts the effects that distance from the central place and patch quality have on dominance and the competitive strategies used by CPFs engaged in contests over access to food patches.

In the following two sections, I briefly present the aspects of Ydenberg & al.'s (1986) model which are relevant to my study.

I.iv The Social Central Place Foraging Model

The basic foraging unit of a CPF is the round trip, composed of patch time (P) during which the individual collects food, and travel time (T) during which it journeys between the patch and its central place (the return trip), and vice-versa (the outbound trip). Energy is gained only during patch time, but is expended during the entire round

trip. The model assumes equal energetic costs for all components, and consequently time can be used as a direct measure of costs. A CPF is assumed to increase its fitness by maximizing its gross RFD to its central place, defined as the weight of the load (W) that it carries back to its central place per unit round trip time (P + T).

While in a patch, the model assumes that prey are loaded at a decelerating rate, due to a loss of efficiency in searching for and handling subsequent prey. Loading effects of this type have been observed in the eastern chipmunk (Kramer & Nowell 1980; Giraldeau & Kramer 1982; Giraldeau & al. in press) and the wheatear, Oenanthe oenanthe (Carlson & Moreno 1982). Different functions can be used to describe a CPF's declining loading rate; following Giraldeau & Kramer (1982), Ydenberg & al. (1986) used a negative exponential function, such that the load size W after a patch time of P is $W(P) = Q \{1 - \exp(-(d[m - c]P))\}$ (Eq. 1), where Q is the horizontal asymptote, set by the maximum capacity of the animal's loading apparatus, $d(m - c)$ is the individual's loading rate, set by the patch's prey density (d) and the animal's foraging behaviour (m - c), and m is the individual's intrinsic maximum loading rate, which can be reduced by the behaviour(s) of conspecific(s) (c).

The contests the Ydenberg & al. (1986) model considers are for patches that yield the highest RFD, termed rich

patches. The model defines interference as any behaviour at a contested patch that reduces the loading rate, and thereby an individual's RFD from the patch (Fig. 1). When the level of interference caused to a competitor is such that the competitor's RFD from the contested patch is lowered below the RFD from alternative food points, the competitor should choose to abandon the contested patch and exploit the set of lower quality alternative foraging sites arrayed around its central place, termed the home set.

According to Ydenberg & al.'s (1986) model, a given level of interference is more effective in depressing a competitor's RFD from a patch at a short than at a long distance from the competitor's burrow (Fig. 2). The reason for this is that with increasing distance, the proportion of a competitor's round trip time spent in travel increases, while the proportion of the round trip time spent in the contested patch decreases; events in the patch -such as interference- then have less impact on the competitor's RFD. Consequently, interference efficiency declines as distance increases. Giraldeau & al. (in press) showed that the presence of conspecific competitors had a stronger effect on the RFDs of individual chipmunks at short than at long distances.

Ydenberg & al. (1986) did not investigate the effect of patch quality (richness) on interference efficiency. But

using their model and the same reasoning, I predict that a given level of interference is more effective in decreasing a competitor's RFD from a poor than from a rich patch (Fig. 3). As patch richness increases, the proportion of a competitor's round trip time spent in travel increases, whereas the proportion of the round trip time spent in the contested patch decreases; events in the patch have less impact on the competitor's RFD. Interference efficiency decreases with increasing patch richness.

Therefore, as distance of the contested patch from the competitor's burrow and/or richness of the contested patch increase(s), a CPF should be less inclined to interfere, trying to exclude the competitor from the patch in order to gain exclusive access, and be more willing to exploit the patch simultaneously with the competitor, trying to maximize its share without direct interference. In other words, the Ydenberg & al. (1986) model predicts a gradual transition from interference to exploitation competition as distance and/or patch richness increase(s).

I.v Objectives

The Ydenberg & al. (1986) social central place foraging model represents an attempt to combine both aspects of economic defendability which characterize studies of territoriality, and predictions on the form of competitive

strategies which characterize the game theoretical study of conflict behaviour. It formulates predictions concerning dominance, and the use and intensity of competitive strategies. The goal of my study was to test the model by investigating the effect of distance and patch richness on the eastern chipmunk's competitive foraging behaviour. I therefore observed in the field dyads of chipmunks contesting access to experimental food patches, that were placed at various distances from burrows and differed in seed density. Ydenberg & al.'s (1986) model predicts that dyad members should have interfered with each other less and be tolerant of one another more, as distance and/or patch richness increased.

II METHODS

II.i Study Area, Subjects and Experimental Patches.

I carried out experiments at the McGill University Research Reserve, Mont St-Hilaire, 35 km S.E. of Montréal, from 16 July to 26 October 1990 and during the entire month of May 1991. The study site consisted of an area of about 2 ha, in a mature mixed-deciduous forest (maple, beech, oak) located on a N. facing slope of a sector to which the public had access (Maycock 1961).

Subjects were fourteen adult eastern chipmunks (7 males, 7 females). Animals were trapped in "Sherman" and "Longworth" live-traps baited with sunflower seeds (Helianthus sp.), marked by ear tags for permanent identification, and by clipping unique patterns of guard hairs to reveal the dark underfur for identification at a distance, weighed (± 0.1 g) and sexed. Burrows were located by following chipmunks through their foraging activities, and identified by plastic tape flags attached to a trunk or a branch near their entrances.

An experimental patch consisted of a food-containing core area surrounded by a foodless 60 cm wide periphery. The core area was made up of two 38 x 15 x 4.5 cm plastic trays placed side by side, each filled with a 1.5 l mixture of "Vermiculite" and sunflower seeds. This mixture approximated natural conditions of food searching in the ground litter by

chipmunks. The periphery was delimited by eight small tent-pegs, and contained no food, either from a natural or a human source.

II.ii Experimental Design

Subjects formed ten dyads (2 male-male, 7 male-female, 1 female-female). Each dyad was composed of a unique combination of a focal animal and a neighbouring competitor. I observed both members contesting an experimental food patch; the patch was placed at an equal distance from each member's burrow. Observations were conducted at four distance categories, within poor and rich patches. Each dyad thus could be observed in eight combinations of distance x patch richness.

Assuming that the population density on the study site was comparable to those reported for other populations in north-eastern North America (Elliott 1978; Getty 1981a), the four distances were chosen in such a way that a chipmunk was likely foraging within: (1) its home range's core area (short category, 10 - 15 m); (2) at the peripheries of its home range (intermediate category, 20 - 25 m); (3) within one neighbour's home range (long category, 45 - 50 m); and (4) within a second neighbour's home range (longest category, 65 - 70 m). Observations were generally recorded at the median distance of the range for each category. Distances were

measured using a compass and a 30 m measuring tape, with an estimated precision to the nearest 0.5 m.

Two extreme patch richnesses were selected to insure that chipmunks experienced different seed loading rates between both categories. The patch's core area seed densities were: (1) 20 g of seeds/l of "Vermiculite" for poor patches; and (2) 200 g/l for rich patches. Preliminary experiments suggested that a chipmunk's average loading rate was likely doubled from poor to rich patch condition (H. Lair pers. com., pers. obs.). To prevent any depletion effect on the loading rate, a new patch was used for each observation in the poor condition. Considering its very high seed density, a rich patch was replaced only after every three patch visits.

II.iii Procedures

Before recording an observation, dyad members had to have met at the patch a minimum of three times within half an hour. Then, when the focal animal and the competitor were both in view, returning to the patch after having unloaded seeds in their burrows, the observer sat quietly on the ground 3 - 4 m from the patch, ready to record an observation. An observation started when the focal animal entered the patch, and ended when it left the patch to travel back to its burrow. When only one dyad member was in view, as soon as it entered the patch, the observer used his hand to

block access to the patch's core area, without chasing the individual out of the periphery. This so-called observer disturbance lasted 30 s. If the other dyad member was in view by the end of this period, an observation was recorded immediately when the focal animal entered the patch.

To prevent conspecific non-dyad neighbours from attempting to forage in the experimental patch, the observer provided seeds near all of the known burrows in the vicinity of the patch. Observations during which a non-dyad chipmunk, a grey or red squirrel (Sciurus carolinensis and Tamasciurus hudsonicus, respectively), a raccoon (Procyon lotor), or a human interfered with the behaviour of the focal animal and/or the competitor were excluded from the analysis.

I recorded the focal animal's behaviour on a portable computer (Radio Shack TRS 80), programmed as an event recorder with a precision to the nearest 0.01 s. The following events were recorded during each observation: time spent in tolerance (T), intolerance (I), alone (A), and outside (O) the patch. Tolerance time was operationally defined as the time during which both dyad members were simultaneously loading seeds in the patch core, including short 1 - 3 s alerts. Time spent in intolerance was defined as the time during which both members were simultaneously in the patch, but only one member could load seeds in the core area. The time during which only the focal animal was in the

patch was defined as the time spent alone. Time spent outside was defined as the time during which the focal animal was neither in the patch nor in travel to its burrow; for example, it occurred when the focal animal was chased out of the patch by the competitor, but came back afterwards without having returned to its burrow to unload seeds.

For each observation, I calculated contact time (C), defined as the total time during which both dyad members were simultaneously in the patch ($T + I$), as well as percent tolerance time, defined as the percentage of contact time spent in tolerance ($[T / C]100$). Finally, the total duration of each observation ($T + I + A + O$), was also calculated.

Statistical analyses were done using SYSTAT (Wilkinson 1989) on a Packard-Bell (IBM compatible) personal computer.

III RESULTS

III.i General

Experiments were conducted on a total of fourteen chipmunks, forming ten distinct dyads (dyads 1 to 6 in 1990 & dyads 7 to 10 in 1991; Table 1). In all, 213 observations were recorded, mostly during the 1990 experiments (140 vs 73 for 1990 & 1991, respectively). Combining experiments for both field seasons provided observations which covered an entire period of a chipmunk's yearly above-ground activity (from May to October); no temporal pattern in their distribution among dyad x distance x patch richness combinations was observed (Table 1). Observer disturbance used to synchronize attendance of dyad members at a patch was required in 56 observations.

Not all possible distance x patch richness combinations were tested from one chipmunk dyad to another. Observations were indeed collected primarily within rich patches at short and intermediate distances (Table 1). Consequently, effects of patch richness and distance could not be analyzed jointly, as they would have confounded each other (Neter & al. 1985). I therefore analyzed effects of both factors separately.

Chipmunks spent an average of 17.61 s (se = 1.03, n = 213, range = 1.00 - 57.24) in contact. Of this contact time, they tolerated competitors for 5.27 s (0.63, 213, 0.00 - 38.77), while they were intolerant of one another for 12.34 s

(0.84, 213, 0.00 - 57.24). Thus, chipmunks spent 18 % (2, 213, 0 - 100) of their contact time in tolerance.

III.ii Distance

III.ii.i The Effect on Percent Tolerance Time

Analyses. Distance effects were analyzed within each patch richness category. In rich patches, for the short-intermediate comparison as well as for the intermediate-long comparison, a two-factor analysis of variance (2-way ANOVA) on the arcsin-transformed percent tolerance time was performed. Distance was used as the factor of interest, and the identity of chipmunk dyads as a grouping factor. In order to have a balanced design, only dyads for which at least four observations were recorded at both distance categories of interest were included in each analysis, i.e. six dyads for comparisons of short and intermediate distances, and four for comparisons of intermediate and long distances (Table 1).

Dyad 5 provided enough trials to compare its percent tolerance time from long to longest distance (Table 1). I used a t-test to evaluate the significance of the effect within this dyad.

Within poor patches, because of the sparse sampling at all distance categories except at the short one, distance effects on percent tolerance time could only be tested by way of t-tests, from short to intermediate category (dyad 3;

Table 1), and from intermediate to long category (dyad 4; Table 1).

Results. Within rich patches, the distance effect on percent tolerance time was not monotonic (Fig. 4). The ANOVAs revealed that chipmunks' percentage of contact time spent in tolerance significantly decreased from short to intermediate distance ($F = 37.84$, $df = 1,65$, $p < 0.001$; Fig. 4), and on the contrary significantly increased from intermediate to long category ($F = 26.98$, $df = 1,40$, $p < 0.001$; Fig. 4). Even though four out of six dyads in the short-intermediate comparison showed a decrease in percent tolerance time (Fig. 4), a significant distance \times dyad identity interaction was noted ($F = 9.85$, $df = 5,65$, $p < 0.001$). As was true in the short-intermediate comparison, there were significant among-dyad differences in the distance effect for the intermediate-long comparison ($F = 9.62$, $df = 3,40$, $p < 0.001$). Three of the four chipmunk dyads increased their percent tolerance time from intermediate to long distance, while only one (dyad 1) decreased it (Fig. 4).

Comparison of percent tolerance time of dyad 5 tested at both long and longest distances is consistent with that found for the intermediate-long comparison. The percentage of contact time the focal animal of dyad 5 spent tolerating its competitor was significantly greater at longest (mean \pm se = 86 ± 5 %, number of observations = 5) compared to long ($68 \pm$

4 %, 5) distance ($t = -2.76$, $df = 8$, $p = 0.025$).

Within poor patches, distance did not have any significant effect, since percent tolerance time in dyad 3 did not significantly vary from short (1 ± 1 %, 8) to intermediate (0 ± 0 %, 5) category, and an analogous result was found in dyad 4 for the intermediate-long (33 ± 12 %, 7; 31 ± 9 %, 7) comparison ($t = 0.12$, $df = 12$, NS).

III.ii.ii The Effect on Components of Percent Tolerance Time

Percent tolerance time is the result of an interplay between tolerance and intolerance times, as well as the sum of these, contact time. There are several ways in which distance can affect these components and lead to variations in percent tolerance time. In the following section then, I investigated the distance effect on each one of these components, using the same statistical analysis procedures as in the previous section.

Contact Time. Contact time was significantly greater at short compared to intermediate distance ($F = 19.03$, $df = 1,65$, $p < 0.001$; Fig. 5), and the distance x dyad identity interaction was not significant ($F = 1.70$, $df = 5,65$, NS). Distance, however, had a significant increasing effect on the time chipmunks spent in contact in the intermediate-long comparison ($F = 24.97$, $df = 1,40$, $p < 0.001$; Fig. 5), while distance and dyad identity significantly interacted ($F =$

9.54, $df = 3,40$, $p < 0.001$). Figure 5 actually shows that, as for percent tolerance time, contact time in dyad 1 varied in an entirely different way than in the other three dyads: only in dyad 1 did it decrease from intermediate to long distance.

The time spent in contact by members of dyad 5 decreased from long (29.69 ± 2.62 s, 5) to longest (26.80 ± 2.63 s, 5) distance, but the difference was not significant ($t = 0.78$, $df = 8$, NS).

Within poor patches, no significant differences in contact time were reported in dyad 3 between short (4.99 ± 0.83 s, 8) and intermediate (8.59 ± 3.28 s, 5) distances ($t = -0.84$, $df = 11$, NS), as well as in dyad 4 between intermediate (31.95 ± 6.67 s, 7) and long (32.15 ± 4.27 s, 7) categories ($t = -0.03$, $df = 12$, NS).

Tolerance Time. Chipmunks spent significantly less time in tolerance as distance increased from short to intermediate category ($F = 15.06$, $df = 1,65$, $p < 0.001$; Fig. 6), while the reverse was true from intermediate to long distance ($F = 42.14$, $df = 1,40$, $p < 0.001$; Fig. 6). The among-dyad variation in the distance effect was significant in the short-intermediate comparison ($F = 5.19$, $df = 5,65$, $p < 0.001$), in which four -out of the six- dyads decreased their tolerance time (Fig. 6). Chipmunk dyads also responded to significantly different extents to increased distance for the intermediate-long comparison ($F = 5.97$, $df = 3,40$, $p =$

0.002). Post-hoc multiple comparisons -with a family level of significance controlled by the Bonferroni method- indicated that distance had a significant increasing effect on tolerance time among dyads 4 ($F = 13.97$, $df = 1,40$, $p = 0.001$), 5 ($F = 11.62$, $df = 1,40$, $p = 0.002$), and 6 ($F = 37.33$, $df = 1,40$, $p < 0.001$), while it had almost no effect at all in dyad 1 ($F = 0.00$, $df = 1,40$, NS). Such an among-dyad pattern (Fig. 6) is similar to those found for percent tolerance and contact times.

As for the intermediate-long comparison, members of dyad 5 tended to tolerate each other more at longest (23.64 ± 3.39 s, 5) compared to long (19.96 ± 1.54 s, 5) distance, although the difference was not significant ($t = -0.99$, $df = 8$, NS).

Within poor patches, distance had no significant effect on the time chipmunks of dyad 3 spent in tolerance from short (0.06 ± 0.06 s, 8) to intermediate (0.00 ± 0.00 s, 5) category; similarly, tolerance time in dyad 4 did not significantly differ from intermediate (14.00 ± 5.48 s, 7) to long (9.76 ± 2.60 s, 7) distance ($t = 0.70$, $df = 12$, NS).

Intolerance Time. From short to intermediate category, distance had a significant decreasing effect on the time chipmunks were intolerant of each other ($F = 10.26$, $df = 1,65$, $p = 0.002$; Fig. 7), and the distance x dyad identity interaction was not significant ($F = 1.31$, $df = 5,65$, NS). The distance effect was not significant for the intermediate-

long comparison ($F = 0.36$, $df = 1,40$, NS; Fig. 7); distance and dyad identity did not interact significantly ($F = 2.48$, $df = 3,40$, NS).

The focal animal of dyad 5 was intolerant of its competitor for significantly shorter periods from long (9.73 ± 1.98 s, 5) to longest (3.16 ± 0.97 s, 5) distance ($t = 2.98$, $df = 8$, $p = 0.017$).

Within poor patches, there was no significant variation of intolerance time in dyad 3 in the short-intermediate (4.92 ± 0.83 s, 8; 8.59 ± 3.28 s, 5) comparison ($t = -0.86$, $df = 11$, NS), and in dyad 4 between intermediate (17.95 ± 3.23 s, 7) and long (22.40 ± 4.26 s, 7) distances ($t = -0.83$, $df = 12$, NS).

III.iii Patch Richness

III.iii.i The Effect on Percent Tolerance Time

Analyses. Analyses on patch richness effects were conducted within each distance category (except at the longest [65 - 70 m]). At short distance as well as at intermediate distance, I used a 2-way ANOVA to investigate the patch richness effect on the arcsin-transformed percent tolerance time. For the same reason as in the 2-way ANOVAs on the distance effect, each analysis included only dyads for which a minimum of four observations were collected in each patch richness condition at a given distance category. Thus,

six and three dyads were considered for the ANOVAs at short and intermediate distances respectively (Table 1).

At long distance, since only dyad 4 was observed in both poor and rich patches (Table 1), I compared percent tolerance time between the two categories using a t-test.

At the longest distance, the absence of data from most cells precluded any statistical analysis of the patch richness effect (Table 1).

Results. Percent tolerance time increased with patch richness at both short (Fig. 8A) and intermediate (Fig. 8B) distances. The ANOVAs confirmed the significance of the effect of patch richness at both short ($F = 87.23$, $df = 1,68$, $p < 0.001$) and intermediate ($F = 9.00$, $df = 1,41$, $p = 0.005$) distances. However, dyads responded to different extents to the change of patch richness category, as indicated by a significant patch richness x dyad identity interaction at both short ($F = 16.59$, $df = 5,68$, $p < 0.001$) and intermediate ($F = 6.21$, $df = 2,41$, $p = 0.004$) distances. At short distance, the majority (4 out of 6) of chipmunk dyads increased their percent tolerance time with patch richness (Fig. 8A); whereas at intermediate distance, post-hoc tests confirmed this result in only one of three dyads (dyad 1: $F = 0.26$, $df = 1,41$, NS; dyad 3: $F = 0.00$, $df = 1,41$, NS; dyad 4: $F = 18.60$, $df = 1,41$, $p < 0.001$; Fig. 8B). Therefore, the statistical significance of the patch richness main effect on

percent tolerance time at intermediate distance remains questionable.

Comparison of percent tolerance time of the dyad 4 tested in both patch richness conditions at long distance agrees with those reported by the ANOVAs. The percentage of contact time spent in tolerance by chipmunks of dyad 4 was significantly greater in rich ($74 \pm 5 \%$, 5) compared to poor ($31 \pm 9 \%$, 7) patches ($t = -3.70$, $df = 10$, $p = 0.004$).

III.iii.ii The Effect on Components of Percent Tolerance Time

As for distance, in order to explain and understand in more detail how patch richness affected percent tolerance time, it was necessary to analyze its effects on contact, tolerance and intolerance times. This was done exactly in the same way as for percent tolerance time.

Contact Time. Contact time tended to be longer in the poor compared to the rich patch category at both short (Fig. 9A) and intermediate (Fig. 9B) distances. As it is demonstrated by the ANOVAs however, the effect of patch richness on the time chipmunks spent in contact just failed to reach conventional levels of significance both at short ($F = 3.89$, $df = 1,68$, $p = 0.053$) and intermediate ($F = 4.04$, $df = 1,41$, $p = 0.051$) distances. Patch richness and dyad identity interacted significantly at both short ($F = 3.48$, df

= 5,68, $p = 0.007$) and intermediate ($F = 7.63$, $df = 2,41$, $p = 0.002$) distances. Within each distance category in fact, not all chipmunk dyads responded to increased patch richness by reducing their contact times. In two of the six dyads at short distance (Fig. 9A), and in one of the three dyads at intermediate distance (Fig. 9B), members actually spent more time in contact in rich compared to poor patches.

At long distance, there was also no significant difference in contact time of dyad 4 between the poor (32.15 ± 4.27 s, 7) and the rich (33.30 ± 1.52 s, 5) patch condition ($t = -0.22$, $df = 10$, NS).

Tolerance Time. Patch richness had different effects on tolerance time at short (Fig. 10A) and intermediate (Fig. 10B) distances. At short distance, chipmunks tolerated each other for significantly longer periods in rich compared to poor patches ($F = 62.26$, $df = 1,68$, $p < 0.001$), while at intermediate distance tolerance time appeared to remain relatively constant with patch richness ($F = 0.32$, $df = 1,41$, NS). There was a significant among-dyad variation in the patch richness effect at short distance ($F = 13.15$, $df = 5,68$, $p < 0.001$), although four of the six dyads increased their tolerance time from the poor to the rich patch category (Fig. 10A). At intermediate distance, two chipmunk dyads showed almost no tolerance time in either patch type, whereas patch richness had a slight decreasing effect on the time

spent in tolerance by members of dyad 4 (Fig. 10B); consequently, the patch richness x dyad identity interaction was not significant ($F = 0.34$, $df = 2,41$, NS).

The only dyad tested in both patch richnesses at long distance responded as those at short distance, spending significantly more time in tolerance in rich (24.61 ± 1.60 s, 5) compared to poor (9.76 ± 2.60 s, 7) patches ($t = -4.39$, $df = 10$, $p = 0.001$).

Intolerance Time. Intolerance time decreased with patch richness at both short (Fig. 11A) and intermediate (Fig. 11B) distances. Unlike for tolerance time, the patch richness effect on the time chipmunks spent in intolerance was significant at both short ($F = 11.63$, $df = 1,68$, $p = 0.001$) and intermediate ($F = 5.85$, $df = 1,41$, $p = 0.020$) distances. The way in which patch richness affected intolerance time did not significantly differ among dyads at short distance ($F = 2.00$, $df = 5,68$, NS); it was in fact rather uniform, five of the six dyads reducing their intolerance time from poor to rich patches, and only one increasing it (Fig. 11A). At intermediate distance, chipmunk dyads responded significantly differently to increased patch richness ($F = 13.34$, $df = 2,41$, $p < 0.001$); post-hoc tests indicated that two dyads showed a significant decrease in intolerance time (dyad 1: $F = 8.29$, $df = 1,41$, $p = 0.006$; dyad 3: $F = 5.28$, $df = 1,41$, $p = 0.027$; Fig. 11B), while one showed a significant increase

(dyad 4: $F = 14.76$, $df = 1,41$, $p < 0.001$; Fig. 11B).

At long distance, chipmunks of dyad 4 behaved as the majority of dyads at both short and intermediate distances, spending significantly less time in intolerance in the rich (8.69 ± 1.95 s, 5) compared to the poor (22.40 ± 4.26 s, 7) patch condition ($t = 2.56$, $df = 10$, $p = 0.028$).

III.iv Dyad Identity

In each ANOVA on the patch richness effect at short and intermediate distances, and in six -out of the eight- ANOVAs on the distance effect, the identity of chipmunk dyads had a significant effect. This means that there was a significant among-dyad variation in percent tolerance time, as well as in its components, regardless of the within-dyad patch richness or distance effect.

IV DISCUSSION

My study shows that both distance from the burrow and patch richness affect the extent to which competing chipmunks tolerate one another at a food patch. On the one hand, distance had a 'V'-shaped effect on percent tolerance time, chipmunks being the least tolerant of each other at intermediate distance. On the other hand, patch richness had an increasing effect on percent tolerance time: the richer the patch, the more likely were chipmunks to tolerate one another.

IV.i Distance

Distance did not seem to have any consistent effect on percent tolerance time within poor patches. However, caution must be exercised here, since results were based on a small sample size (2 dyads), such that it would be necessary to conduct additional studies on the effect of distance in poor patch conditions.

Within rich patches, distance had a significant yet complex effect on percent tolerance time. Chipmunks decreased their percent tolerance time from short to intermediate distance, and increased it from intermediate to long distance, as well as from long to longest distance. This result is at odds with most of the commonly characterized social spacing patterns (Lott 1991).

The distance effect on percent tolerance time in rich patch conditions, especially the initial decline in the short-intermediate comparison, appears to contradict many empirical studies on space-related dominance. For example, it has been observed in several studies, dealing with a wide variety of animals, that the dominance status of individuals depends on the location at which interactions take place. Studies conducted with chipmunks (Dunford 1970; Elliott 1978; Yahner 1978) showed that in an encounter such as a contest over a food patch, an individual was more likely to initiate and win a chase (be dominant) when it was closer to its burrow than was the opponent to its burrow. Thus, a chipmunk within its core area -i.e. within around 12 m of its burrow- usually dominates over all conspecifics, while at greater distances, it apparently could either ignore other chipmunks and concentrate on resource exploitation, or become subordinate (be chased) if foraging within a conspecific's core area (references as above; also Getty 1981a).

It is important to point out that all these studies on the chipmunk's and other animal's social spatial organization, unlike the present study, failed to control for the relative distances of the contestants to their central places. In chipmunk studies, for instance, considering the approximate average interburrow distance (25 - 35 m; Elliott 1978; Getty 1981a), when one individual was close to the

centre of its dominion, the intruder, by definition, must have been further. The dominance status of competitors was then probably the result of the effect of asymmetries in distance rather than the effect of distance *per se*. Ydenberg & al. (1986) demonstrates how unequal travel distances to the contested patch may lead to payoff asymmetries between foragers, that can account for the observed space-related dominance characterizing chipmunk sociality.

However, their social central place foraging model also makes a prediction on the effect of distance alone. It predicts a gradual transition from interference to exploitation competition as distance increases, irrespective of any distance-related payoff asymmetry between contestants; that is, in chipmunks, tolerance should be at its minimum close to the burrow, gradually shifting to its maximum further away. The current study controlled for distance asymmetries by presenting patches at equal distances from the burrows of both competitors of a dyad. The results, therefore, represent the first true indication of the effect of distance *per se* -not asymmetries in distance- on the chipmunk's competitive strategies. They showed that the pattern exhibited by chipmunks from short to intermediate distance, is the exact opposite of the model's prediction: percent tolerance time decreased with distance. Consequently, the effect of distance on the use and intensity of

competitive strategies in CPFs, such as chipmunks, seems unlikely to be explained, following Ydenberg & al.'s (1986) model, by the economical consequences of increased travel time.

It is possible that the results I observed are the simple product of an owner-intruder uncorrelated asymmetry. For example, the reduced percent tolerance time at intermediate distance may have been caused by one chipmunk being in its home range while the other was not. Although the chipmunk's home range usually has a roughly circular shape with the burrow as its approximate center, deviations from this pattern occur (Elliott 1978). Hence, the transect which was chosen to measure distance categories, may not have crossed the home ranges of the two members of a dyad in a symmetrical fashion. At short distance, the contested patch was certainly in an area of overlap between both chipmunks' home ranges, while at intermediate distance it may have been included in only one home range, its owner then having a higher dominance status and being less tolerant of its conspecific competitor at that latter category. Mapping of the chipmunks' home ranges would have been a non negligible improvement to my experimental design.

Not surprisingly, as distance became greater chipmunks then increased their percent tolerance time. An individual's normal home range likely covers foraging movements of 10 - 15

m (short) and 20 - 25 m (intermediate category) from the burrow (Elliott 1978); however, when the patch was at long and longest distances, contests surely took place in an area well beyond the limits of the home ranges of both members of a dyad. Chipmunks were probably a lot less familiar with this area and may have been more at risk of attack by non-member conspecifics or even predators, thus being less inclined to waste foraging time by interfering with each other. Clarke & al. (1993), for example, found that chipmunks took more time to reach a refuge when they were released outside their home ranges as opposed to within their home ranges.

It has often been observed that territorial residents respond less intensely to an intrusion by a neighbour than by a stranger (Ydenberg & al. 1988). In the present study, each dyad was always composed of direct neighbours. Considering the average interburrow distance in dyads studied in my experiments, when the patch was at short distance chipmunks were probably foraging at the peripheries of their core areas, i.e. in a shared 'boundary' zone intermediate between their burrows. Natural encounters between chipmunk neighbours occurred mostly in this zone (Elliott 1978). At intermediate distance, however, the patch may have been at a location where neighbour-stranger contests were likely to be naturally common, whereas neighbour-neighbour contests were not. Ydenberg & al. (1988) showed how the asymmetric war of

attrition (a game theory model) can explain the neighbour-stranger effect. Following their reasoning, it is possible that the two competitors of a dyad may have not recognized each other and behaved as if they were less familiar -and consequently more aggressive- with one another when contesting the patch at intermediate as compared to short distance, resulting in the initial decline in percent tolerance time.

Percent tolerance time is the result of an interplay between three variables: tolerance, intolerance, and contact times. The time spent in tolerance was very likely a pertinent and reliable measure, with regard to the extreme smallness of the area in which both members of a dyad had to be feeding together. Intolerance time, meanwhile, may have not reflected precisely the extent of interference used by competitors. My experimental design actually, did not discriminate between active interference and waiting. At short distance for example, intolerance time may have been spent mostly in active interference where chipmunks were constantly pushing their way into the patch's core area; both dyad members may have tried so much to get access to the seeds that they had to tolerate one another at some point. At intermediate distance on the contrary, interference may have involved fewer interactions, simply because one of the individuals spent its time primarily waiting in the patch

periphery for the other's departure from the core area; (almost) no tolerance may have occurred then. It is possible that such an imprecision in the operational definition of intolerance time, may have affected the relevance of percent tolerance time as a measure of the use and intensity of competitive strategies. In future studies, it would be therefore important to distinguish between the different types of interference behaviour at a patch, so as to detail the effect of distance on chipmunks' competitive strategies.

IV.ii Patch Richness

Compared to distance, patch richness had a more straightforward effect on percent tolerance time. At short, intermediate, and long distances, chipmunks were proportionally more tolerant of each other in rich than in poor patches, the most significant effect of patch richness being at short category. These results are consistent with the Ydenberg & al. (1986) central place foraging model's prediction: animals gradually should be more involved in exploitation rather than interference competition as patch richness increases, i.e. tolerance should be greater in rich than in poor patch conditions.

The effect of patch richness on percent tolerance time may be closely related to a great number of studies on feeding territoriality, in which the relationship between the

optimal territory or home range size and food abundance was specifically examined (Lott 1991; Milinski & Parker 1991). By comparing my results and those of Mares & al's (1982) study of a chipmunk population for instance, a parallel can be drawn between the degree of exclusive use of a patch (on a time scale) and of a home range (on an spatial scale) by an individual chipmunk. Mares & al. (1982) manipulated food availability and/or population density, and found that individuals had smaller home ranges when food supply was superabundant. In the current study, the increased percent tolerance time in rich patches implies that at least one of the members of a dyad spent proportionally less time foraging alone in the patch core when the seed density was high. Thus, an individual chipmunk had a smaller 'exclusive' foraging area as the environment richness increases (Mares & al. 1982), and correspondingly, had a less exclusive access to/use of a rich than a poor patch.

The increase in percent tolerance time with patch richness may indicate that poor patches are more defensible than rich patches. Lair & al. (in press) reported that when individual chipmunks are forced to wait before entering a patch, they begin searching for and sampling the quality of alternative sites at lower levels of imposed waiting time when the patch is in a poor as compared to a rich condition; furthermore, they allocated more time to that environmental

tracking. These results, like mine, may suggest that the richer the patch, the less likely it is defensible. It is worth noting that such an interpretation seems to contradict game theory studies on conflict behaviour, in which the duration and intensity of fighting in contests increase with the value of the resource (e. g. Enquist & Leimar 1987).

Independently of any economical consideration, the increase in percent tolerance time from poor to rich patches may be traced to the different foraging patterns of individual chipmunks in the patch's core area when patch richness varied. In the low seed density condition, animals moved more from one place to another within the core area, i.e. both within and between the two trays; moreover, even when an individual remained in one spot, it tended to move his head more and dig in the "Vermiculite" more. Movements were much less frequent and intense in the high seed density condition. As a result, increased movements to search and load seeds when foraging in poor patches, meant that dyad members were more likely to be close enough to interfere actively than when foraging in rich patches. Indeed, modifying the movement patterns during foraging may have acted as the mechanism through which individual chipmunks responded to changes in patch richness. This possibility raises the following question, which is somewhat related to the effect of spatial clumping (Monaghan & Metcalfe 1985;

Grant & Guha 1993): would the results have been the same if poor patches had been larger than rich ones, i.e. if patch richness had been changed by varying the area (the number of trays) over which the same weight of seeds was distributed, instead of varying the weight of seeds which was distributed over the same area? Such a question should be answered in the future.

IV.iii Dyad Identity

The identity of chipmunk dyads had a significant effect in most of my analyses. This may have been due to a variation, from one dyad to another, in the familiarity between members: more familiar chipmunks were probably less aggressive with each other. Among-dyad variations in sex, age, and dominance status, may also have been likely responsible for the dyad identity effect. Thus, these factors -i.e. individual differences- must be taken into account and controlled in studies of foraging models.

IV.iv Conclusion

The goal of my study was to investigate the effect of distance and patch richness on the eastern chipmunk's competitive foraging behaviour. Although the results on the effect of patch richness were in accord with the Ydenberg & al. (1986) central place foraging model's prediction, the

model failed to predict successfully the effect of distance. On the one hand, the model is by necessity an oversimplified representation of the reality, and may have omitted some factors that could account for the effect of distance and/or patch richness on dominance and the competitive patch exploitation strategies used by chipmunks. On the other hand, percent tolerance time may not have been the most pertinent measure to estimate the change from one type of competition to the other. In order to test the model's actual predictions in a more accurate way, future studies should, among other things, measure detailedly the interference behaviours used by contestants so as to discriminate between exploitation competition, waiting, and active interference.

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Table 1. The number of focal animal observations, and the date of recording, for each dyad x distance x richness combination.

Burrow-patch distance categories (m)								
Dyad iden- tity	Patch richness categories							
	Poor	Rich	Poor	Rich	Poor	Rich	Poor	Rich
1	-	-	10 08/31	10 08/23	-	4 08/28	-	-
2	-	11 09/24	-	3 10/02	-	-	-	-
3	8 07/30	5 08/14	5 07/30	10 08/15	-	-	-	-
4	-	-	7 09/07	5 08/01	7 09/11	5 09/10	-	-
5	7 08/02	5 07/31	2 09/19	5 07/25	-	5 07/26	1 07/27	5 07/27
6	-	6 09/20	-	6 09/21	-	8 09/25	-	-
7	6 05/10	5 05/01	-	5 05/23	-	-	-	-
8	5 05/14	11 05/02	-	6 05/20	-	-	-	-
9	5 05/11	6 05/05	-	7 05/19	-	-	-	-
10	6 05/29	11 05/28	-	-	-	-	-	-

Figure Legends

Figure 1. The effect of interference on the RFD. Theoretical loading functions are derived from Eq. 1, with $Q = 4.6$, $d = 5$, $m = 0.025$. For undisturbed loading (full line), $c = 0$, and when loading with interference (dashed line), $c = 0.015$. The optimal load size is found by drawing the tangent from the travel time to the curve. When there is interference, the optimal load size decreases ($W_{ni} > W_i$) but patch time increases ($P_{ni} < P_i$); therefore, the optimal RFD -given by the slope of the tangent line- is lower.

Figure 2. The effect of distance on interference efficiency. Loading curves as in Fig. 1. Competitor β travels a longer distance to the contested patch than competitor α . The extent of the decline in the RFD due to interference -given by the angle formed by the tangents to the no interference and interference curves- is smaller for animal β than for animal α .

Figure 3. The effect of patch richness on interference efficiency. Theoretical loading functions are derived from Eq. 1, with $Q = 4.6$, $m = 0.025$. For rich patches (thick lines), $d = 5$, and for poor patches (thin lines), $d = 1$. For undisturbed loading (full line), $c = 0$, and when loading with interference (dashed line), $c = 0.015$. Competitors β forage in a richer patch than competitors α . The angle formed by tangents to the no interference and interference curves of each patch type give the extent of the decline in the RFD due to interference. The angle for poor patches (ΔRFD_{α}) is greater than for rich patches (ΔRFD_{β}).

Figure 4. The relationship between percent tolerance time and distance, in rich patches. Each point is a treatment cell mean (+ se), i.e. a dyad x distance combination mean (+ se). Each pair of identical symbols, linked by a full line, is a chipmunk dyad, for which at least five replicates were collected in each distance category of interest. Dyads are indicated as follows open diamonds: 1; open circles: 3; closed diamonds: 4; closed stars: 5; closed triangles: 6; open squares: 7; closed circles: 8; open stars: 9.

Figure 5. The relationship between contact time and distance, in rich patches. Points and symbols as in Figure 4.

Figure 6. The relationship between tolerance time and distance, in rich patches. Points and symbols as in Figure 4.

Figure 7. The relationship between intolerance time and distance, in rich patches. Points and symbols as in Figure 4.

Figure 8. The relationship between percent tolerance time and patch richness categories, at short (a) and intermediate (b) distances. Each point is a treatment cell mean (+ se), i.e. a dyad x patch richness combination mean (+ se). Each pair of identical symbols, linked by a full line, is a chipmunk dyad, for which at least five replicates were collected in each patch richness category. Dyads are indicated as follows open diamonds : 1; open circles: 3; closed diamonds: 4; closed stars: 5; open squares: 7; closed circles: 8; open stars: 9; closed squares: 10.

Figure 9. The relationship between contact time and patch richness categories, at short (a) and intermediate (b) distances. Points and symbols as in Figure 8.

Figure 10. The relationship between tolerance time and patch richness categories, at short (a) and intermediate (b) distances. Points and symbols as in Figure 8.

Figure 11. The relationship between intolerance time and patch richness categories, at short (a) and intermediate (b) distances. Points and symbols as in Figure 8.

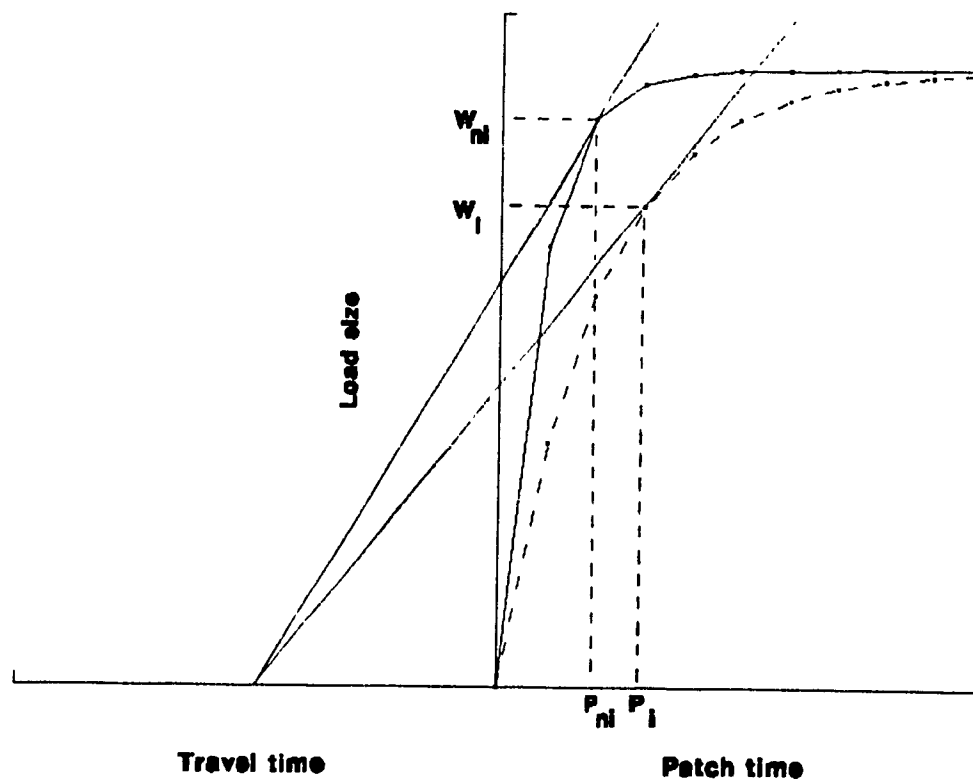


Figure 1

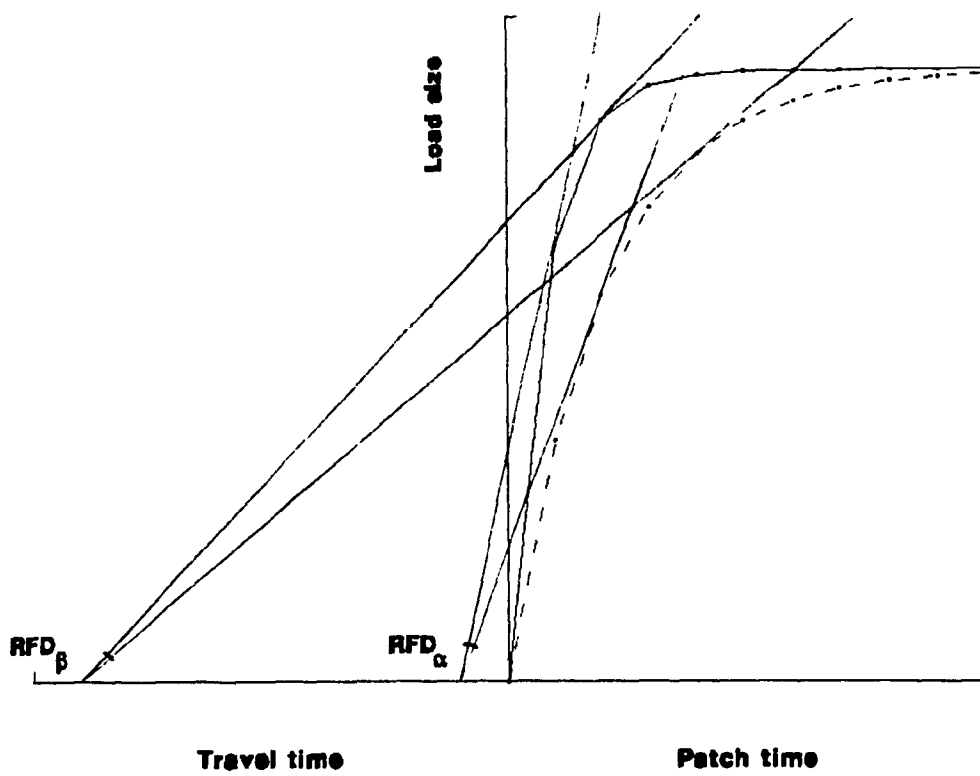


Figure 2

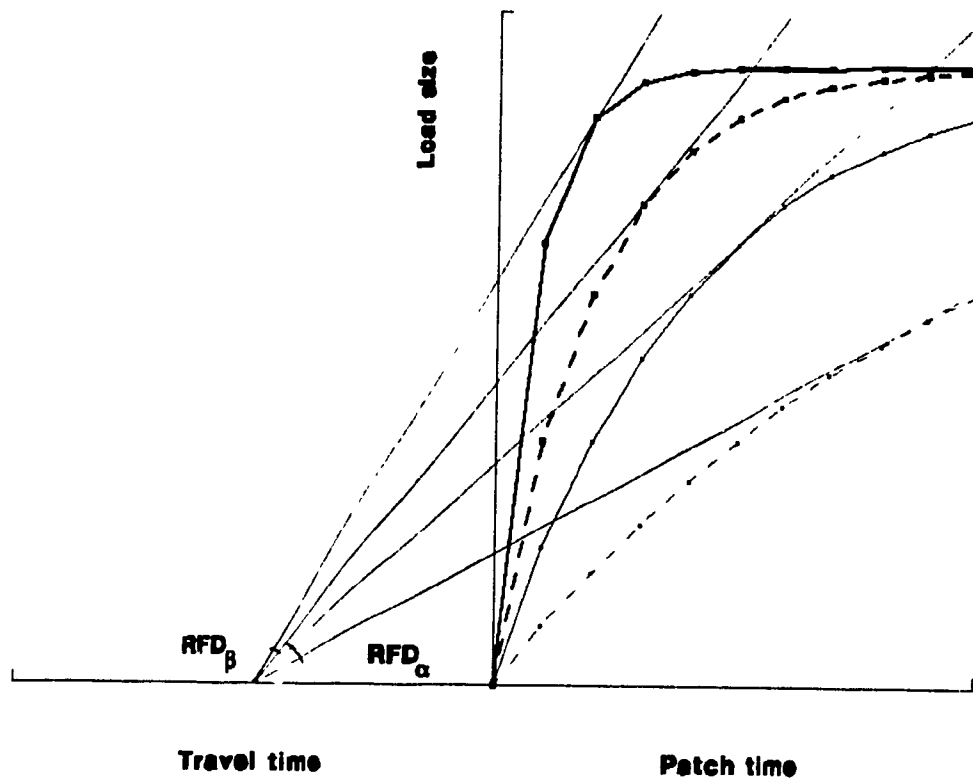


Figure 3

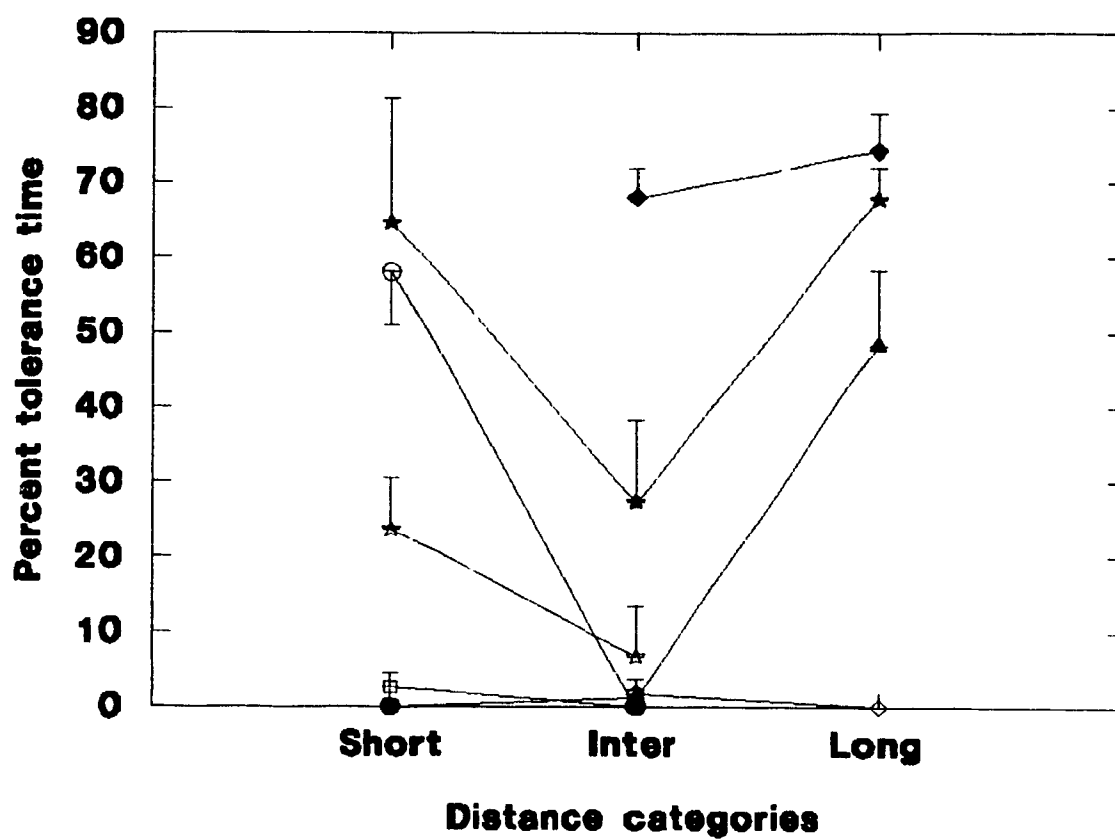


Figure 4

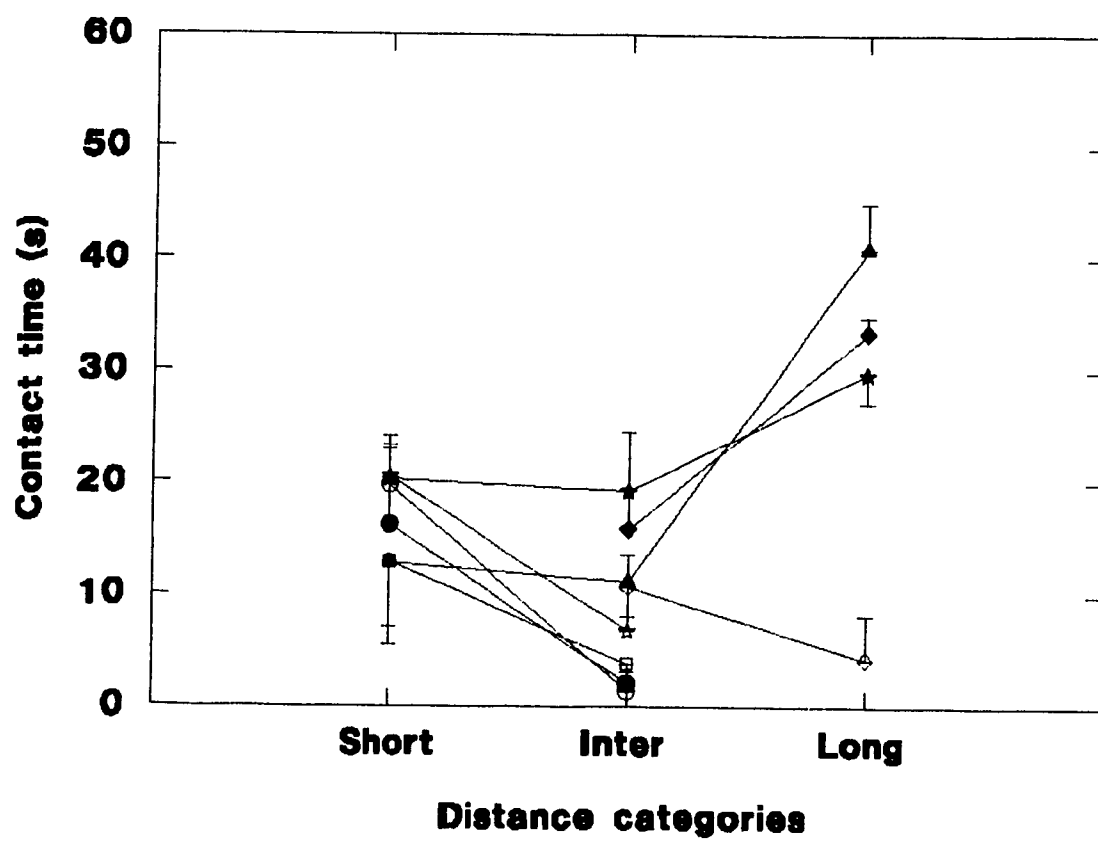


Figure 5

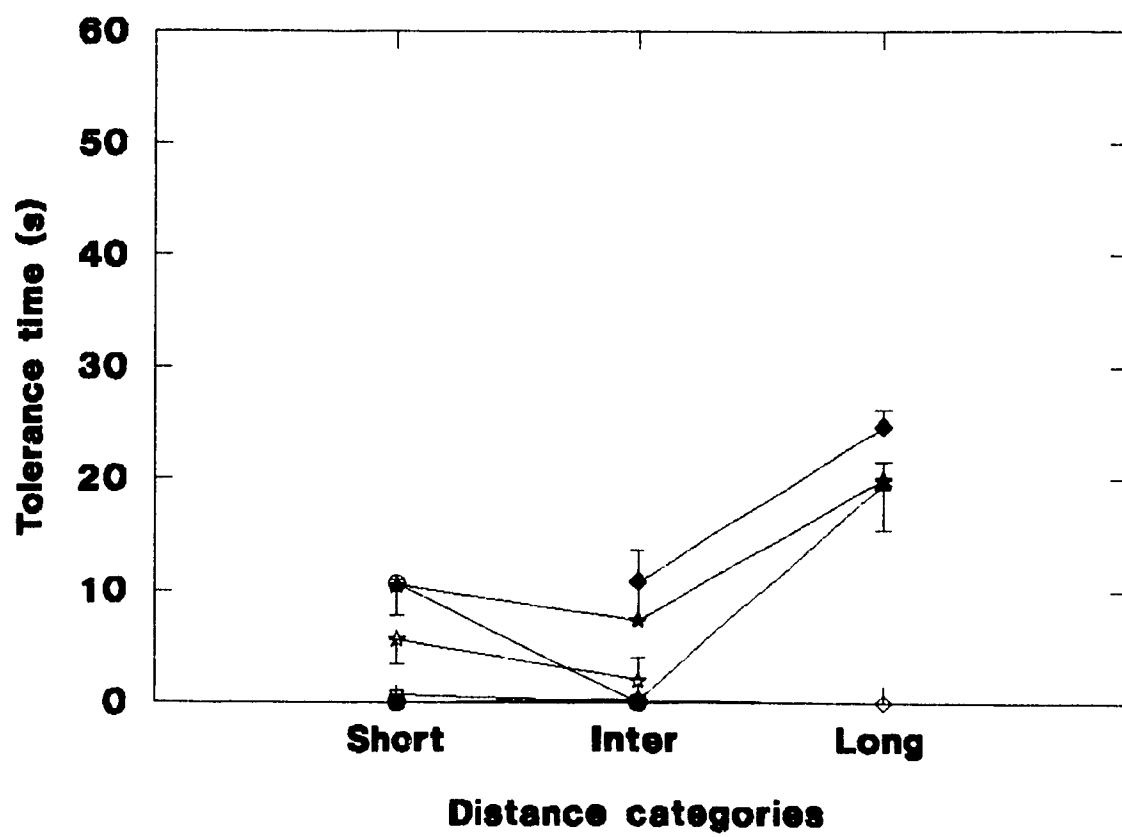


Figure 6

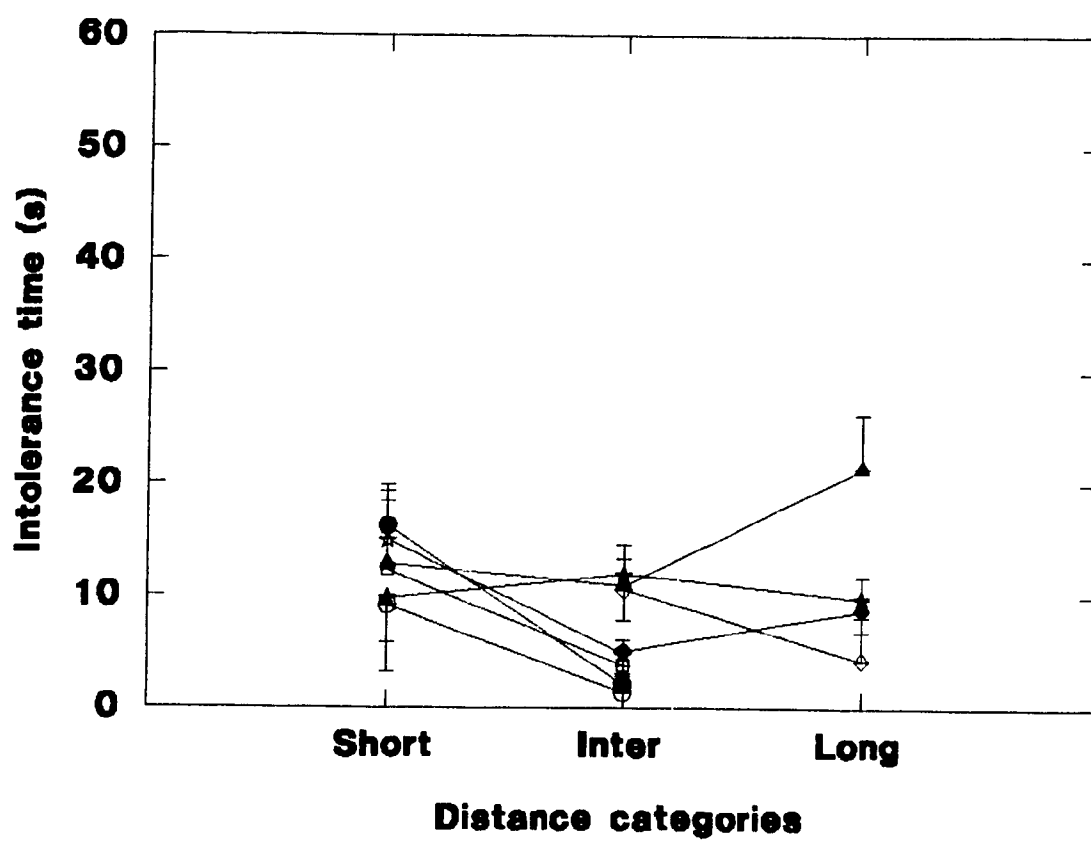


Figure 7

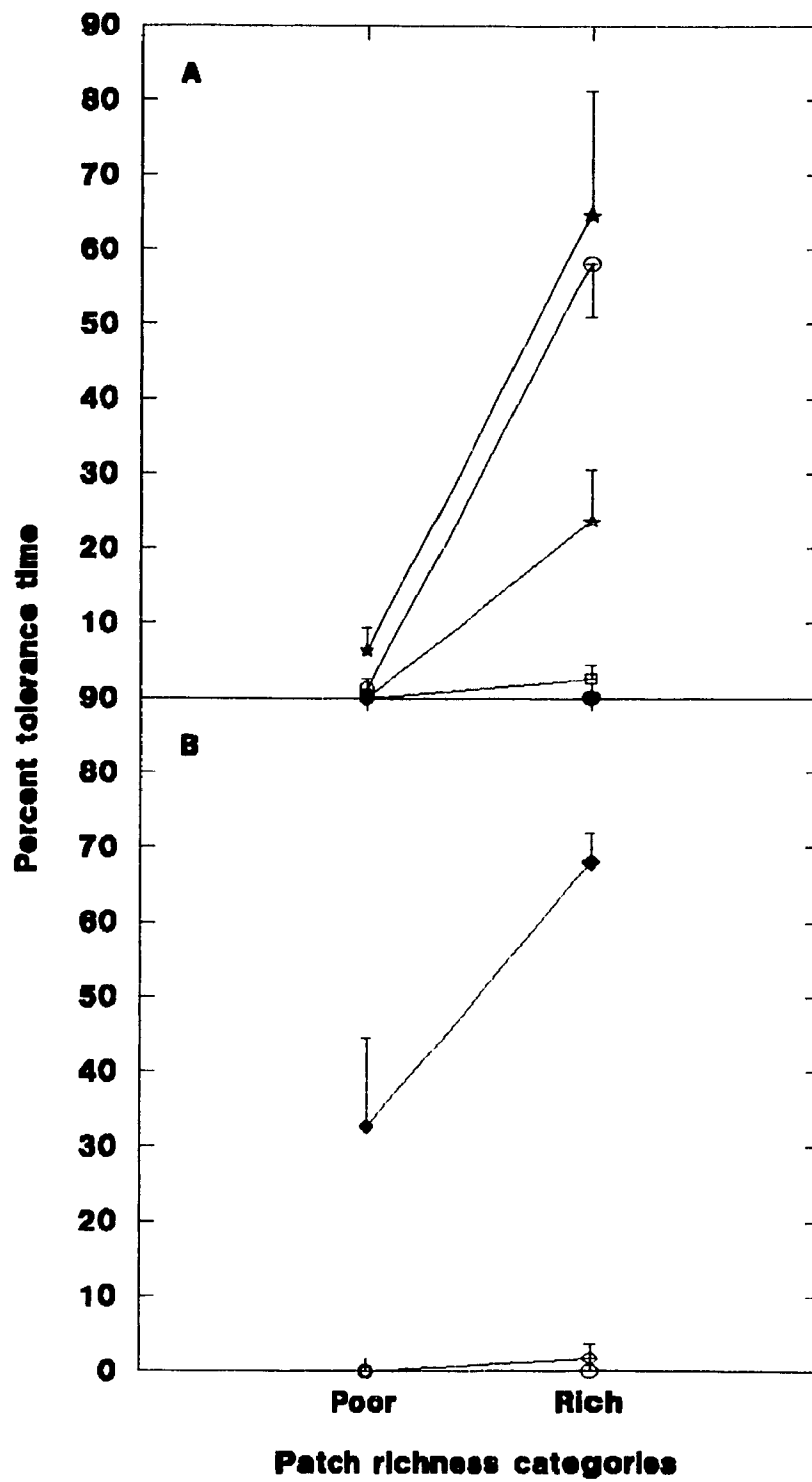


Figure 8

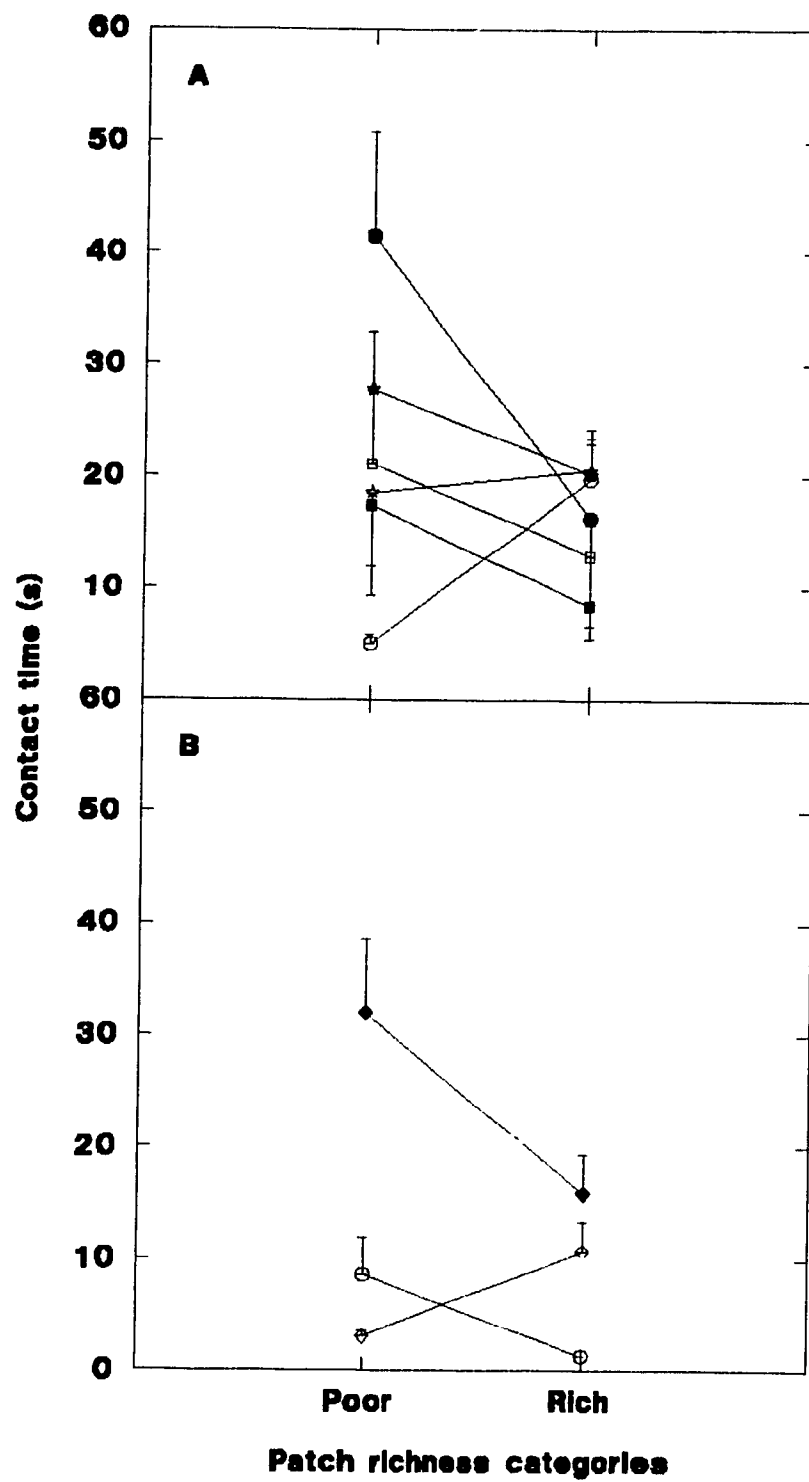


Figure 9

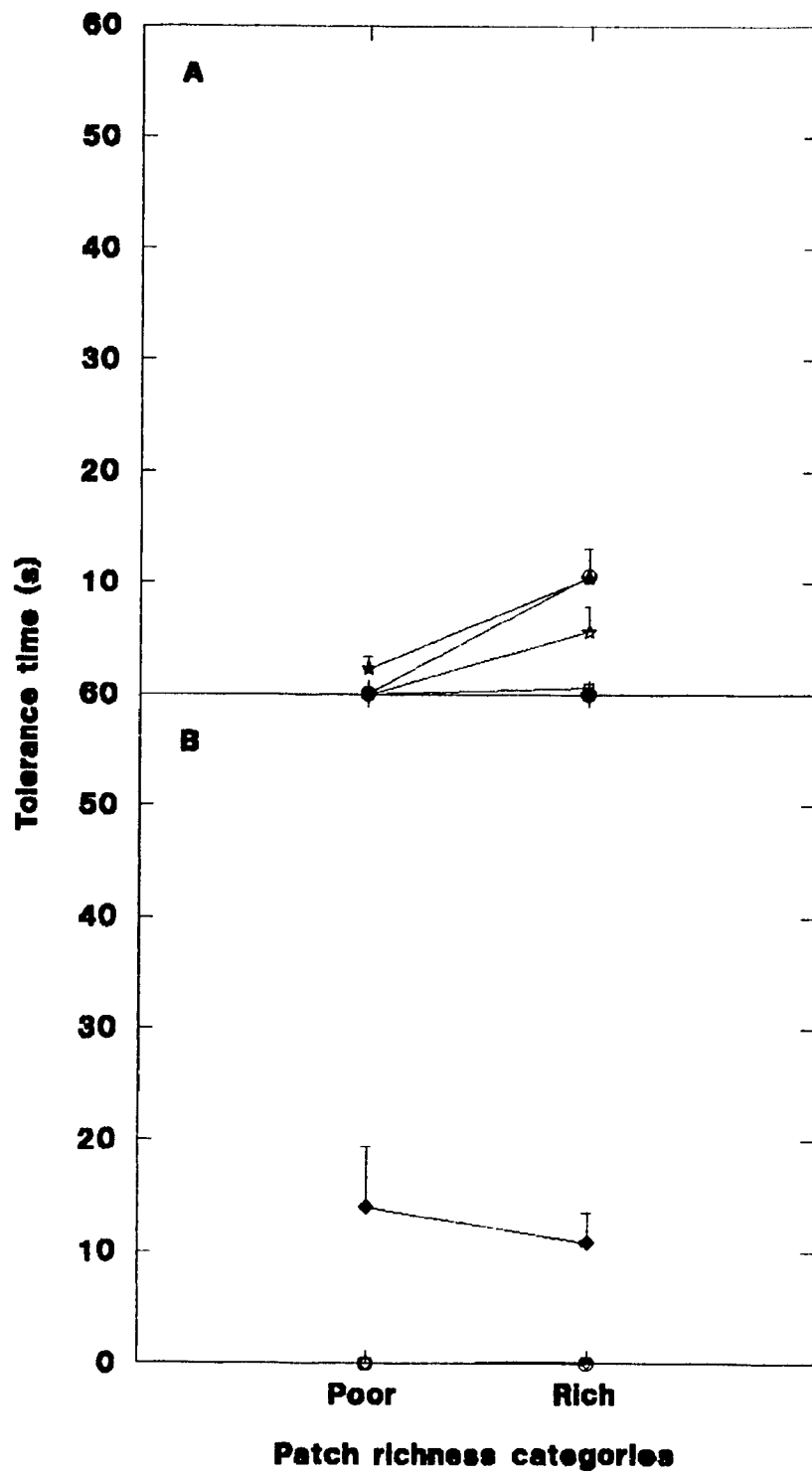


Figure 10

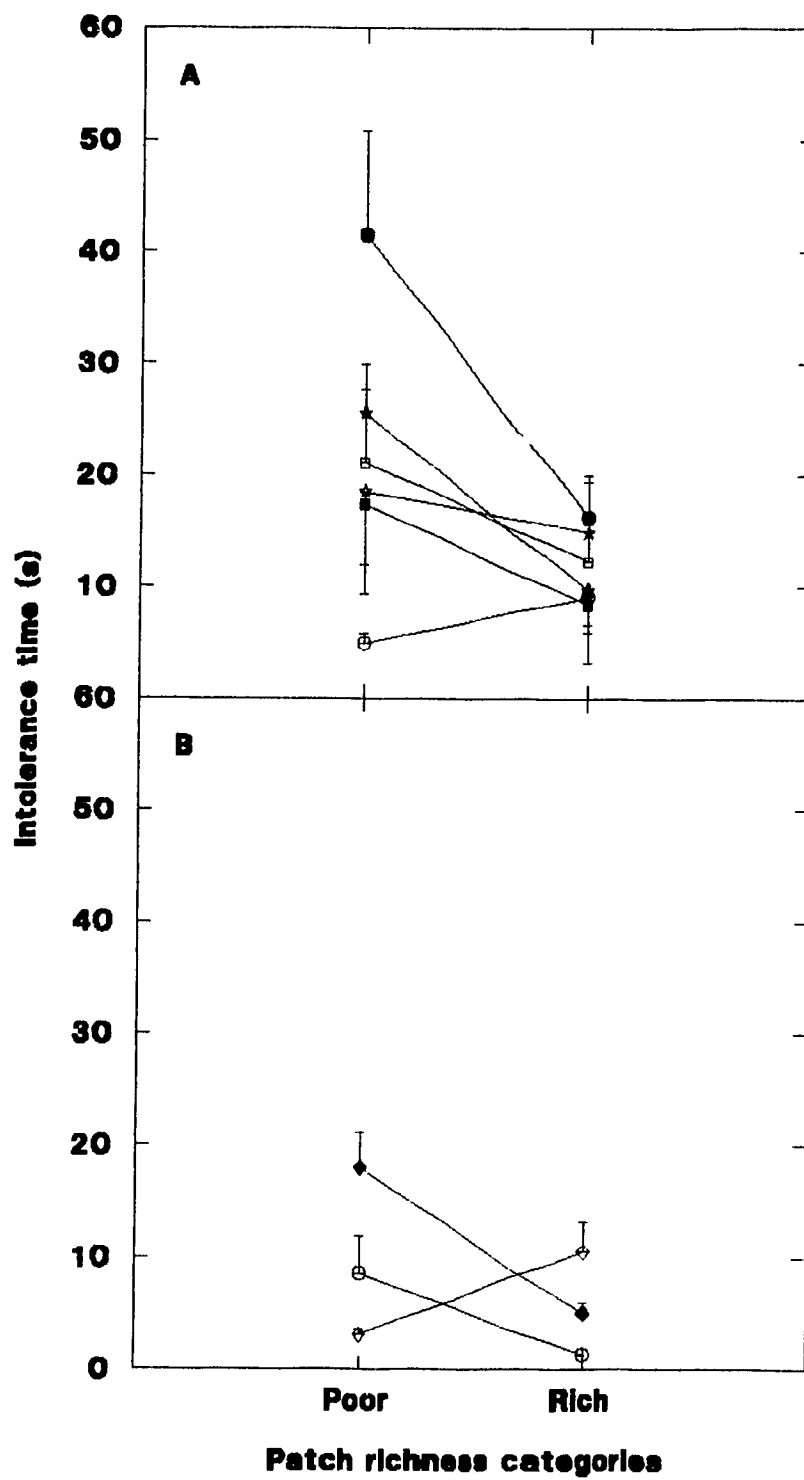


Figure 11