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Non-Resource Based Territoriality in Males of the Butterfly *Xamia xami* (Lepidoptera: Lycaenidae)

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In the Pedregal de San Angel reserve, in Mexico City, males of the butterfly Xamia xami *perch in and defend areas with well-defined topographic limits. These areas lack concentrations of receptive females and of larvae and adult resources. One individual defends the same territory an average of 5 h/day, up to a maximum of 23 days. The same areas are used as territories by different males during the year. These areas share some characteristic features which are described. Evidence is presented in support of the hypothesis that the territories function as mating stations. A possible scenario for the evolution of this territorial mating system is advanced.*

KEY WORDS: *Xamia xami*; Lycaenidae; butterfly territoriality; mating systems.

INTRODUCTION

Butterflies exhibit a great diversity of mating systems (Rutowski, 1984; Alcock, 1985, 1987). In one of the most intriguing types, males defend areas that lack receptive females or resources attractive to receptive females (Thornhill and Alcock, 1983; Bradbury, 1985; Alcock, 1987). Apparently females come to these territories just to mate. Several authors have discussed the evolution of this kind of mating system (Emlen and Oring, 1977; Parker, 1978; Baker, 1983; Thornhill and Alcock, 1983; Bradbury, 1985). The most widely accepted explanation advanced to date is that this sytem will evolve when receptive females are scarce and widely dispersed and their resources evenly distributed. Under these conditions monopolization of mates through defense of females or

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resources attractive to them will be impossible, and an evolutionary alternative open to males is the defense of "conventional encounter sites" where females come solely to mate. For females there is an advantage in coming to such places because this reduces their mate-searching or their mate-comparison costs. Usually these territories are located on landmarks [e.g., hilltops (Shields, 1967; Alcock, 1987)].

In this paper we document the territorial behavior of males of the butterfly *Xamia xami* and describe in detail the physical characteristics of the territories. Then, on the basis of our data and other ecological information (Ziegler and Escalante, 1964; Benrey, 1986; Soberon *et al.*, 1988), we propose a possible scenario for the evolution of this territorial mating system.

MATERIALS AND METHODS

The study site is located in a small area (124 ha) maintained as an ecological sanctuary by the Universidad Nacional Autonoma de Mexico, in the south of Mexico City. This area is part of the Pedregal de San Angel, a community characterized by a rough volcanic soil, a markedly seasonal rainfall regime, and xerophytic shrubby vegetation (Rzedowski, 1954; Alvarez *et al.*, 1987).

Xamia xami is a multivoltine butterfly which can be found throughout the year in low numbers (Soberon *et al*, 1988). Its principal larval food plant at our study site is *Echeveria gibbiflora* (Crassulaceae), a perennial plant abundant in the area (Soberon *et al.*, 1988).

Observations were made on 107 days distributed between December 20, 1983, and March 31, 1985. Behavioral data were recorded using focal sampling (Altmann, 1974). Males were identified by conspicuous natural wing marks (tearings and/or descaled areas) or by marks made on the wings with indelible (Sharpy) felt-tip pens. Naturally marked and ink-marked individuals did not differ noticeably in survival or behavior. The daily observation periods of each individual varied between 0.5 and 2.0 h, depending on the number of territories occupied that day (the more territorial males were present, the less time was dedicated to each). Observations were made during the active period of adult butterflies, roughly, 1000–1600.

In order to determine the occupation frequency of each territory and the number of days that a given male occupied a territory, we walked through the study area recording the presence and identity of territorial males. Not all territories were identified as such from the beginning of observations (a total of 37 territories were detected and described), so the occupation frequency estimations are based on different numbers of days. Another methodological problem is that it was not always possible to mark the butterflies the first day we saw them. Therefore the number of males seen once (=249) is overestimated and thus, in some cases, the territory tenure time underestimated. A total of 55 males was marked and observed more than once.

RESULTS

Territorial Behavior

In the morning ($\bar{X} \pm$ SD = 0955 ± 43 min; range, 0901–1032; $n = 8$), males arrived at particular places and perched on vegetation until early afternoon ($\bar{X} \pm$ SD = 1511 ± 52 min; range, 1424–1620; $n = 4$). Almost all individuals observed more than 1 day returned day after day to the same place (Fig. 1). We witnessed only one shift between perching sites and very rarely saw males away from perching places.

During the site occupation period, males spent most of the time perching but they flew occasionally, either spontaneously (= noninteractive flights) or in order to investigate passing organisms (= interactive flights), as shown in Table I. There are different kinds of interactive flights. (1) Inspection flights are brief approaches by the perching male to the passing butterfly, after which the resident returns to its perch and the intruder leaves without exhibiting any evident change in behavior. (2) Horizontal flights are pursuits along a horizontal plane, intercalated with periods in which both individuals fly around each other in tight circles. (3) Chases are long, rapid pursuits in which the intruder increases its flight speed when approached by the resident. (4) Spiral flights are interactions during which the resident and the intruder spiral closely about one another

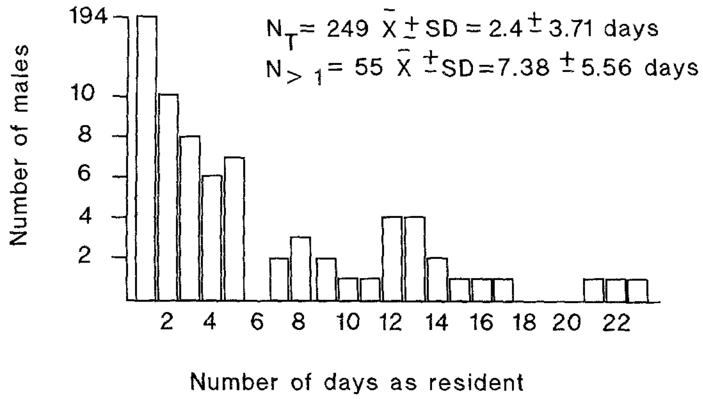

Fig. 1. Frequency distribution of residence time of males on territories. N_T = total number of males (see Materials and Methods); $N_{>1}$ = number of males observed more than one day.

Table I. Time Budget of Territorial Males[a]

	Activity							
	Perching		Noninteractive flights		Interactive flight against heterospecifics		Interactive flights against *X. xami*	
	$\bar{X} \pm$ SD	Range	$\bar{X} \pm$ SD	Range	$\bar{X} \pm$ SD	Range	$\bar{X} \pm$ SD	Range
% total observation time[b]	97.9 ± 1.8	92.1–100	0.93 ± 0.85	0.0–3.6	0.61 ± 0.6	0.0–1.96	0.46 ± 0.98	0.0–4.95
% time occurring inside territory[c]	97.6 ± 6.3	72.7–100	98.4 ± 5.5	76.2–100	98.9 ± 3.3	87.2–100	43.5 ± 34.9	0.0–100
% time occurring outside territory[c]	2.4 ± 6.3	0.0–27.2	1.6 ± 5.5	0.0–23.8	1.1 ± 3.3	0.0–12.8	56.5 ± 34.9	0.0–100

[a] Based on observations of 24 territorial males. Total observation time, 1418.5 min.

[b] Percentage of total observation time.

[c] 100% = total minutes in which activity was performed.

along a vertical or diagonal axis; the height reached by the pair varies between 2 m and high enough to be out of sight.

The type of interactive flight observed in a particular encounter depended on the identity of the intruder (Table II). Inspection flights not followed by other types of interaction were observed almost exclusively (96.7% of events) when the intruder was a heterospecific butterfly; all other types of interactive flights were preceded by an inspection flight not included in Table II. On the other hand, horizontal flights were directed mainly toward conspecifics (33%) and members of the Plebeiinae subfamily (= blues) (63%). Chases and spiral flights were intraspecific interactions. Our results suggest that the function of the inspection flight is to identify the intruder.

We interpret horizontal flights, chases, and spiral flights as aggressive interactions aimed at excluding conspecific males. This hypothesis is consistent with the fact that in all such intraspecific interactions (75% of 146 records), the final result was that one individual was repelled from the area, whereas the other stayed. In all the cases in which it was possible to identify the individual that stayed (83% of 110 records), it was the original resident.

The above interpretation has at least two problems. First, in 85% of intraspecific aggressive interactions ($n = 110$), we were not able to identify the sex of the intruder. Considering the information available for other territorial butterflies (Baker, 1983; Alcock, 1987; Cordero, 1986), we believe the hypothesis that interactive flights are aimed first to identify and then to exclude conspecific males to be probably true. However, chases are similar to mate-refusal flights described in females of some species (Wiklund, 1982; Rutowski, 1984).

The second problem is related to the fact that two-thirds of the horizontal flights occurred against blues (25% of 146 aggressive interactions records).

Table II. Frequency of Different Types of Interactions Between Territorial Males and Different Kinds of Territory "Intruders"[a]

	Type of flight (%)				
Intruder identity	Inspection flight	Horizontal flight	Chase flight	Spiral flight	Courtship flight
X. xami[b]	2.2	29.6	75	86.1	0
X. xami ♂	1.1	3.7	25	13.9	0
X. xami ♀	0	0	0	0	100
Plebeiinae	36.3	63	0	0	0
Other butterflies[c]	60.4	3.7	0	0	0
n	91	54	20	72	14

[a] The percentage of the total number of times in which a given flight type occurred is given in each cell (columns add to 100).

[b] Sex nondetermined.

[c] *Pterourus multicaudatus*, *Anthanassa texana*, *Danaus* sp., and several Pierid species.

These butterflies are the most closely related and similar in size to *X. xami* of all the heterospecific interactant butterflies recorded. Two hypotheses to explain this behavior are that (a) both species compete for the territory or (b) *Xamia* males mistake blues for conspecifics. It is not possible to evaluate (a) without a detailed knowledge of the resource requirements and behavior of the blues. However, we have never observed blues behaving in a territorial way within *X. xami* territories. On the other hand, in at least 17% of the *Xamia*-blue aggressive interactions ($n = 36$) the blue remained in the territory (in 58% of these interactions we did not record whether the blue stayed or left), which supports (b), because if they were competing for the territory it would not be likely that both individuals would share it.

Although the perching areas of the territorial males had a diameter of no more than 1 m, the area from which conspecifics were excluded (= territory) is much bigger and has stable limits. Territorial limits were defined with reference to the behavior of resident males. Territorial males never finished their inspection flights beyond these limits and, in many cases, finished them on the limits. With the exception of the time when they were interacting with conspecifics, territorial males spent most of the time inside their territories (Table I). The limits of these generally coincided with conspicuous topographic features (see the following section).

Territory Characteristics

The same places were used as territories by different males. Since laboratory-kept males never lived more than 36 days [$\bar{X} \pm \mathrm{SD} = 31.34 \pm 1.18$ (Jiménez and Soberón, 1989)], it is certain that males from different generations used the same territories (see Fig. 2 and Table III). These defended places had a number of common features. In general the behaviorally defined limits coincided with terrain features (Fig. 3) such as walls, rocks, bushes, or trees. Thus the territory resembles an "arena" or an "amphitheater." These amphitheaters may be small gullies, areas of low vegetation surrounded by walls and/or rocks and/or high vegetation (bushes and trees), path segments with high vegetation on bothsides, or niches of buildings. When the territory was in a gully it had topographic limits all around. When on a plane, in most cases (18 of 22) it had well-defined topographic limits on at least three sides (Fig. 3).

Another trait shared by practically all territories (35 of 36) was their localization on or beside natural or manmade paths, like long stripes of low vegetation or dirt trails (Fig. 3). The shape of territories and their orientation with respect to the path was variable. However, most of them (84%) had an oval shape, with the longest axis parallel to the path. Territory size was highly variable (Fig. 4) and did not show any relationship with occupation frequency ($r_s = 0.24$, $P > 0.1$; Table III).

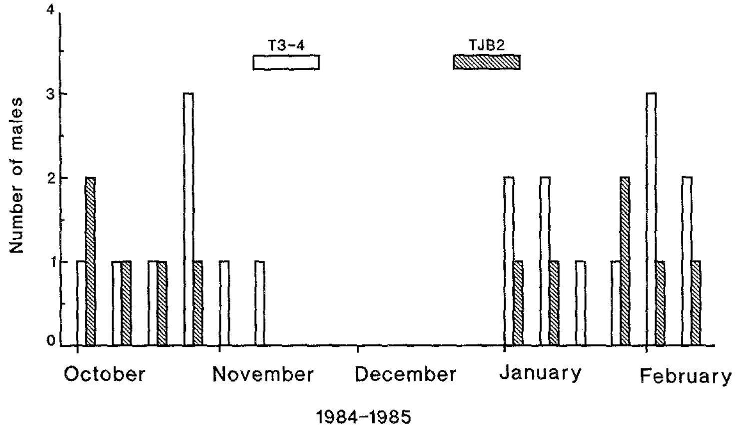

Fig. 2. Number of different males that occupied two typical territories (T3-4 and TJB2) per week over a period of 18 weeks.

Most territories (36 of 37) were defended even in times when there were no nectar sources. Larval food plants (*Echeveria gibbiflora*) were absent in 62% of territories. Moreover, just two of the territories with a high occupation frequency had *E. gibbiflora*, and in very low numbers [considering that in the study area the average *Echeveria* density is more than one plant per m^2 (Soberón *et al.*, 1988)]: 6-7A, two plants; and JB2, three plants.

Table III. Temporal Patterns of Occupation of Different Territories

Territory[a]	No. of days examined	No. of days occupied	Frequency of occupation[b]	No. of males[c]	No. of days/male (range)	Size (m^2)	No. of copulations
3-4 N	107	86	0.80	41	1-23	11.22	3
6-7 A	76	52	0.68	31	1-13	8.91	1
H	32	15	0.47	12	1-8	14.28	
5-6 S	76	35	0.46	35	1	6.21	3
JB2	66	26	0.40	17	1-5	4.80	3
7-8 E	68	20	0.29	11	1-12	13.80	
5-6 N	76	9	0.12	8	1-2	6.97	
6-7 B	68	7	0.10	5	1-5	12.48	
3-4 S	107	9	0.08	4	1-8	28.35	
7	68	4	0.06	4	1	4.56	
6	76	4	0.05	4	1	5.70	

[a] Only territories visited by researchers more than 30 days are considered.
[b] Frequency of occupation = (number of days occupied)/(number of days examined).
[c] This figure is an overestimation because not all males were marked the first day they were observed.

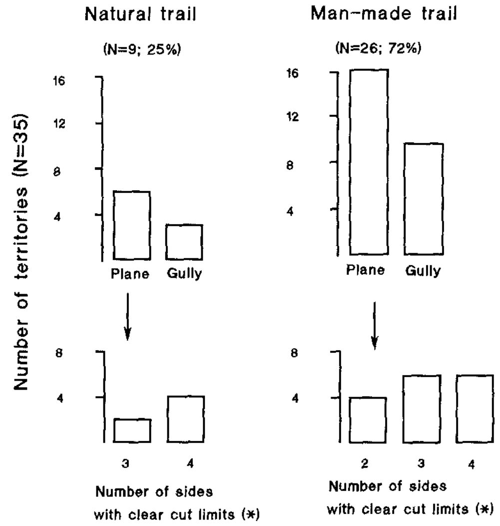

Fig. 3. Topographic features of territories. (*) In these graphs we consider four-sided territories. Territories in gullies have clear-cut limits all around.

Male-Female Interactions

We observed 18 matings, 12 from the onset. All of them occurred inside territories and, with one exception, with resident males. The exception was a male that occupied and mated inside territory T56S, while the original resident (the one that had been in the territory since early morning) was mating with another female.

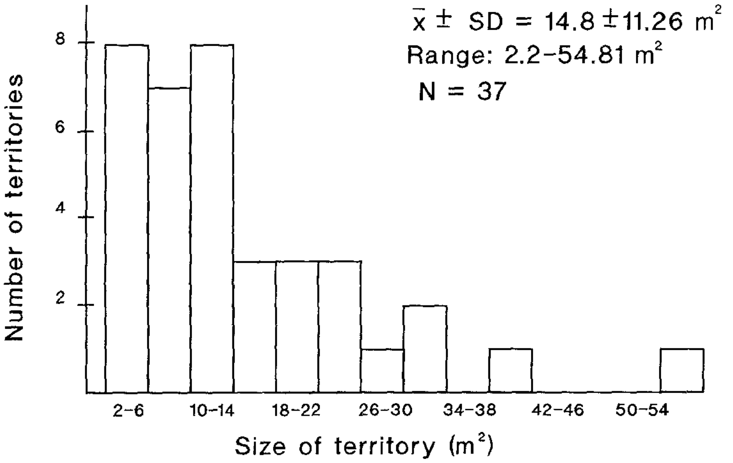

Fig. 4. Frequency distribution of size of territories.

DISCUSSION

Adaptive Value of Territoriality

Non-resource based territoriality by male butterflies has been interpreted as a mating strategy (Thornhill and Alcock, 1983; Rutowski, 1984). However, data concerning the mating advantages of territoriality are scarce (Davis, 1978a; Lederhouse, 1982; Wickman and Wiklund, 1983; Wickman, 1985). In most cases territories are located on landmarks where, supposedly, receptive females come to mate. According to mating systems theory (Emlen and Oring, 1977; Thornhill and Alcock, 1983) this kind of system evolves when (a) receptive females or resources attractive to them are widely dispersed, and (b) females occur at low numbers throughout a relatively long breeding season.

Our interpretation of the behavior of *Xamia xami* males agrees with the above generalizations. Territorial behavior seems to exclude other males which could be sexual competitors of the resident. Although data on mating frequency are scanty, all the matings observed were within territories, which supports the hypothesis that territories are mating stations. It could be argued that these results are biased because observations were concentrated on territories. However, during other work on *X. xami* (Soberón *et al.*, 1988) teams of two to four people walked throughout the study area 2 to 4 days per week for 1 year (October 1983–October 1984), from 0900–1000 to 1200–1300, looking, among other things, for butterflies. Matings were never observed outside territories. Males were observed very rarely outside territories.

The ecological conditions that theoretically should lead to the evolution of this kind of mating system (a and b above) are present for *X. xami*. First, although larval food plants are very abundant in the area, just a small fraction of them are used by ovipositing females. Females tend to lay one egg per plant, using mainly isolated plants (Soberón *et al.*, 1988); and mortality between egg and adult stages in high (Benrey, 1986). Second, the nectar sources are widely dispersed in the area, and finally, females are present all of the year at very low numbers (Soberón *et al.*, 1988). Together, these factors result in a highly dispersed population of ovipositing, emerging, and feeding females.

In contrast with many other landmark-defending butterfly species, *X. xami* males do not defend hilltop territories, at least in our area. We hypothesize that, in the Pedregal de San Angel, the amphitheater character of territories and their location on or beside paths turned these into nodes of receptive female transit (Bradbury and Gibson, 1983). The shape and orientation of territories could help to increase the probability of female detection by residents. From such a situation selection might favor the adoption of these places as conventional mate encounter sites (Parker, 1978; Thornhill and Alcock, 1983). We do not have the behavioral data on receptive females necessary to explore this question. Such data are difficult to collect because of the rarity of females (they are much more difficult to detect in the field than males) and the rough terrain that hinders observation of mobile females.

The Ecology of Mate Location in Landmark-Based Mating Systems

To understand why a population exhibits a particular mating system, it is necessary to consider all the theoretical alternatives open to it (Maynard Smith, 1978). Alcock (1985, 1986, 1987) has recently documented intra- and interspecific differences in male behavior exhibited by hilltopping butterflies (see also Shields, 1967). Variability may also be present in species whose mating sites are not hilltops (Scott, 1975, 1982–1983; Dennis, 1982; Wickman and Wiklund, 1983; Shreeve, 1984, 1987; Wickman, 1985). In these species males show at least four mate location strategies which seem to be a combination of extreme values of two variables: degree of aggressiveness and degree of mobility (Alcock, 1985; Cordero, 1986). Thus, the resulting strategies are (a) aggressive perching (= non-resource based territoriality), (b) aggressive patrolling, (c) nonaggressive perching, and (d) nonaggressive patrolling. These strategies can be species specific (Alcock, 1987), can be present in the same population under different conditions (Wickman and Wiklund, 1983; Alcock and O'Neill, 1986; Alcock, 1987), or can be found simultaneously in a population (Dennis, 1982).

Alcock (1985) advanced a hypothesis based on population density differences to explain male behavioral variability. The predictions of his model are shown in Fig. 5a. Alcock stated that although the conditions that favor (c) or (d) over each other are not clear, thermoregulatory factors could be important. In a recent paper, Alcock (1987), following Bradbury's multivariate approach (1985), considered female choice as a second explanatory factor of the variability of other ecological and behavioral traits of hilltopping insects. We believe that a fuller understanding of (intra and/or interspecific) variability at mate encounter sites requires the addition of another axis to Bradbury's (1985) multidimensional space. This variable is the size of mate encounter sites, relative to the mobility of males and to their ability to detect conspecifics over long distances.

According to the above ideas, the degree of aggressiveness should be inversely dependent on population density. Depending on the evolutionary history of the population, density-sensitive behavioral flexibility may be present or absent. This relationship follows from standard territorial defense theory (Davis, 1978b; Thornhill and Alcock, 1983), according to which the costs of territorial defense at high densities are higher than the benefits. Alcock (1987), Alcock and O'Neill (1986), and Wickman and Wiklund (1983) have documented this density-dependent behavioral shift in *Chlosyne californica, Strymon melinus*, and *Pararge aegeria*, respectively.

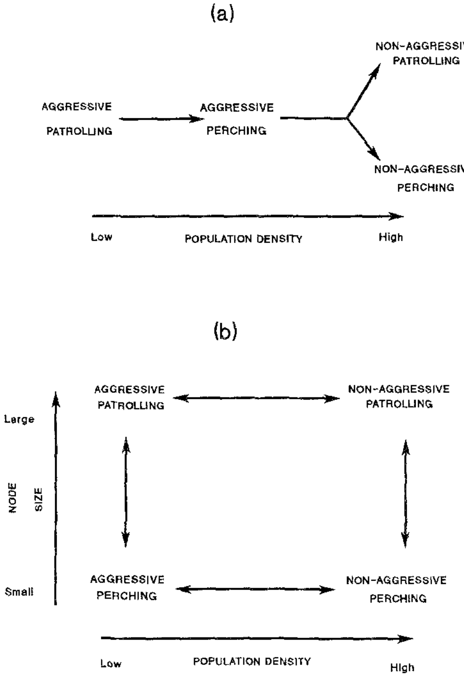

Fig. 5. Two models for mate-location strategies. In the model of Alcock (1985) (a), population density is the main factor. In the model presented here (b) a second factor is the size of the territory or node relative to the sensory capabilities of the male.

On the other hand, the way of searching (perching vs. patrolling) should be a function mainly of the size of the mate encounter site. When the site is small, the resident can detect all the females and intruders that enter the area by just staying in one place. As the size of the mating site increases, the probability of missing a female or an intruding male increases and, thus, the benefits of patrolling. Therefore the degree of mobility should be directly related to the size of the mate encounter site.

There are several factors that may determine the size of mate encounter sites. The structure of the landscape has been shown to be important in some species, for example, *Aglais urticae*, *Inachis io* (Baker, 1972), and *X. xami* territories have well-defined topographic limits (see Fig. 3). There are, however, other species in which territory limits do not appear to coincide with topographic features, such as *Coenonympha pamphilus* (Wickman, 1985). In such species female behavior will determine the size of the mate encounter site. If, for example, the encounter site is in a node of female transit [a "hot spot" (Bradbury and Gibson, 1983)], and females came into it following a few routes (see Fig. 6a), the node size will be smaller than if females arrive from many directions (Figs. 6b and c). In Fig. 6, the area of high probability of finding a female (hatched area) increases as the number of incoming routes increases. The routes used by females should depend on factors such as distribution of resources and whether or not they use landmarks as guides (Thornhill and Alcock, 1983; Bradbury, 1985).

If we combine both relations (aggressiveness-population density and way of searching-node size), we obtain the picture in Fig. 5b. Since density and the size of mate encounter sites vary continuously, intermediate or mixtures of strategies are expected.

X. xami in the Pedregal de San Angel is a low-density species in which the size of the mate encounter site is small, since one male is able to exclude all intruders and detect all the females that enter in it by just staying perched. Given these conditions, the aggressive perching observed in *X. xami* is correctly predicted by our scheme.

The size of at least some territories in our area can be manipulated by removing or adding "topographic limits," and it is also possible to manipulate

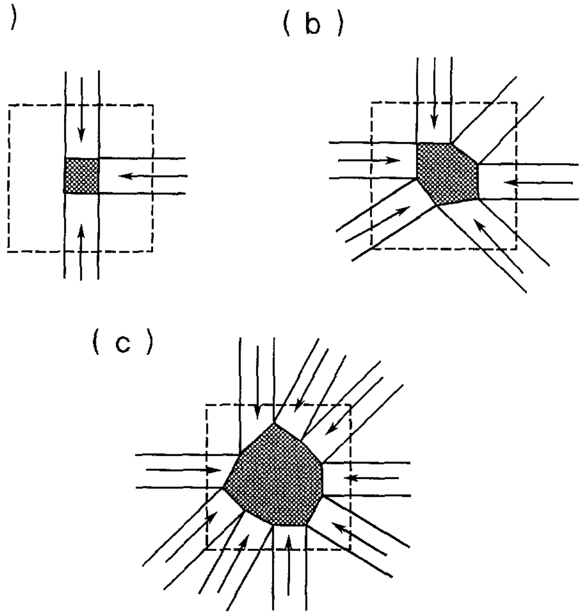

Fig. 6. Effect of the number of routes followed by females in moving through the habitat on the size of female transit nodes (hatched area). Transit nodes are areas of relatively high probability of finding a female.

the frequency of encounters of the territorial male with both males and females. This can be done by releasing *X. xami* individuals, which can be reared in the laboratory (Jimenez and Soberon, 1989) in the vicinity of territories. Therefore it should be possible to test experimentally our hypothesis. This will be attempted in the near-future.

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