

WHY DO SOME MALE *CALLOPHRYS XAMI* (LYCAENIDAE) SHIFT THEIR TERRITORIES?

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ABSTRACT. In a Mexican population of the butterfly *Callophrys xami* at least 13% of the males defended two or more territories sequentially. There were two observed causes of territory shifts by males: aggressive displacement from their territories by other males ($n = 2$), and spontaneous shift to a different territory ($n = 3$); however, in 26 territory shifts the causes were not determined. Evidence suggests that territories were in short supply during the study and, therefore, more territory shifts may have been the result of aggressive displacement. The spontaneous shifts suggest that some males may move in search of a better territory after occupying one of low quality.

Additional key words: behavioral variation, male competition, territoriality.

In several butterfly species, males defend territories that are employed exclusively for male display, mate location and courtship (Rutowski 1991). Variation in territorial behavior in butterflies has been studied mainly in the context of alternative mate location strategies within a species (Davies 1978, Dennis 1982, Wickman 1985, 1988, Alcock & O'Neill 1986, Dennis & Williams 1987, Alcock 1994), although some authors have also discussed the basis for differences between species in territorial vs. nonterritorial mating systems (Alcock 1985, Dennis & Shreeve 1988, Cordero & Soberón 1990, Wickman 1992).

Although intraspecific variation in the number of territories sequentially defended by male butterflies has been documented (Alcock 1985, Knapton 1985, Alcock & O'Neill 1986), it has been specifically discussed in only one study (Robbins 1978). In some species, males spontaneously shift territory as a consequence of their normal migratory movements (Baker 1972). In non-migratory species there are at least two hypotheses to explain territory shifts; these hypotheses and some of their predictions are summarized in Table 1.

In this paper, variation in the number of territories sequentially occupied by individual males of *Callophrys xami* Reakirt (Lycaenidae) is reported, and some of its possible causes and consequences are explored.

MATERIALS AND METHODS

The study was conducted in a 146.8 ha ecological preserve within the main campus of the Universidad Nacional Autónoma de México, in Mexico City. This area is part of the Pedregal de San Angel, and is characterized by volcanic soil, rough topography, markedly seasonal rainfall, and xerophytic shrubby vegetation.

Callophrys xami is a multivoltine butterfly that in the Pedregal de San

TABLE 1. Two hypotheses to explain why males of non-migrant butterfly species might shift territories that they already occupy, and some predictions of these hypotheses.

Hypothesis A: Males shift territories as a result of being aggressively displaced from their previous territories by intruder males.

Prediction A1: Aggressive displacement of territorial males should be observable.

Prediction A2: Successful territory holders (monoterritorial males) should be males with high resource holding power and, therefore, they should tend to be larger, more agile or more experienced than less successful territory holders (polyterritorial males).

Prediction A3: Polyterritorial males, as a result of their displacement from high quality territories, should have a lower copulation success than monoterritorial males.

Prediction A4: The incidence of territory shifts as a result of aggressive displacement should be higher when male density and, therefore, competition for territories is high.

Hypothesis B: Males shift territories because they evaluate their current territories and voluntarily move in search of better ones.

Prediction B1: Voluntary (spontaneous) territory shifts should be observable in territorial males.

Prediction B2: Polyterritorial males should shift, on average, towards territories of higher quality (i.e., those with higher copulation rates).

Prediction B3: Polyterritorial males, as a result of having spent some time in territories of poor quality, should have a lower copulation success than monoterritorial males.

Prediction B4: Male density should be inversely correlated to the probability of finding an unoccupied territory of high quality, and therefore the cost of voluntary territory shift should be lower when density is low, and the probability of changing territory should be higher.

Angel can be found at varying densities throughout the year (Soberón et al. 1988). The population reaches peak density from October to January, although it is never abundant (Soberón et al. 1988). The main larval food plant is the perennial *Echeveria gibbiflora* D. C. (Crassulaceae), which is abundant in the area (Soberón et al. 1988). Males are territorial and defend areas with well defined topographical limits, located beside or on natural or manmade trails; these areas lack concentrations of receptive females and larval or adult food resources (Cordero & Soberón 1990). Males actively defend their territories by means of different types of aggressive flights, for an average of five h per day (between 1000 and 1500), and spend the rest of the time feeding and resting outside territories (Cordero & Soberón 1990). Territories are occupied year after year and function as mate location and courtship stations (Cordero & Soberón 1990, Cordero unpubl. data). Other details of courtship behavior are given in Cordero (1993).

A total of 159 territorial males was captured, individually marked on the wings with indelible felt-tip pens and their right forewing length measured with a caliper through the mesh of the net. Individuals were assigned to one of three wing-wear categories: 1 = similar to a recently emerged adult

(wings mostly green); 3 = very worn male (wings mostly brown with worn margins); and 2 = individuals intermediate between 1 and 3.

Observations were made between 1 November and 20 December in 1989, and between 10 November and 6 December in 1990. The number of territories observed was 25 in 1989 and 19 in 1990; the number of days a territory was visited varied between 25 and 38 in 1989 and between 14 and 24 in 1990. Observations were made in two ways: by walking along transects joining groups of territories at least two times per day, on 31 days in 1989 and 11 in 1990, and observing each territory for a brief time; and by continuous observations through the daily territorial period in a group of occupied territories, during nine days in 1989 and 13 days in 1990.

RESULTS

Most marked males were observed defending only one territory (86/99 males in 1989 and 52/60 in 1990; hereafter, monoteritorial males). Twenty-one males were observed sequentially occupying more than one territory (hereafter, polyterritorial males); these males represented 13.2% of all marked males. Thirteen males occupied two territories, six males occupied three, and two males occupied four. Therefore, a total of 31 territory shifts was detected; however, the exact date of shifts was only determinable for 26 events. The median number of days polyterritorial males occupied each territory was 1 (1.5 in fourth territory, $n = 2$); however, the range varied from <1 day to 14 days in their first territory ($n = 20$), to 1 to 2 days in their fourth territory ($n = 2$) (Table 2). Only one of the 55 marked males observed more than one day in 1983–1985 occupied more than one territory, probably as a result of aggressive displacement (Cordero & Soberón 1990). Territories seem to be in short supply for the males of this butterfly, at least during peaks of male density. In 14 of 17 cases, the site that a male had left was occupied by a different male the same day or the day after.

Direct support for Prediction A1 (Table 1) was provided by two cases in 1989, in which the cause of territory shift clearly was aggressive displacement of the polyterritorial male by an intruder (for description of aggressive interactions see Cordero & Soberón 1990). Two other cases in 1989 probably involved aggressive displacement and resulted in a territory shift. In the first case an aggressive interaction was observed after which a male not previously in the territory began or continued defending it; less than an hour later, the male that had been defending this territory for the three previous days was observed defending a new territory. In the second case, a male was observed for over an hour defending a territory, and then suddenly a different male was in residence; the first male was found defending a different territory 4.5 hours later.

One way of testing Prediction A2 is by comparing the wing length (a measure of size and, possibly, resource holding power) and wing wear (a possible measure of age and experience) of males that are polyterritorial as a result of aggressive displacement with that of monoterritorial males; however, the small number of aggressive displacements observed in this study prevents statistical analysis. In one of three observations of aggressive displacement, the winning male was bigger (1.65 vs. 1.48 cm) and older (2 vs. 1), and in another it was smaller (1.55 vs. 1.62 cm) and younger (1 vs. 3) than the displaced male; data for the third case were not known. Of the two cases of probable aggressive displacement observed in 1989, the winning male was bigger in one (1.72 vs. 1.69 cm) and smaller (1.49 vs. 1.63 cm) in the other. These scant observations neither support nor contradict Prediction A2.

Since virtually all males observed during the course of this and previous studies (since 1983) were territorial or were apparently trying to get a territory, the proportion of territories occupied in a given day was used as a measure of male density (Fig. 1). In 1989, the proportion of territories occupied decreased through the study period ($r_s = -0.887$, $P < 0.001$, $n = 35$), but in 1990 no significant differences were observed in the proportion of territories occupied ($r_s = -0.305$, $P > 0.05$, $n = 17$). Territory shifts were observed throughout the study periods in both years (Fig. 1). Contrary to Prediction A4, aggressive displacement was observed or suspected at both high and low densities in 1989.

Regarding Hypothesis B (Table 1), we observed three cases of spontaneous territory shifts (Prediction B1). In 1989, territorial male *c* moved from territory 3-4S to the contiguous territory 3-4N while inspecting a heterospecific butterfly, and perched in 3-4N without being detected by male *b* (who had been defending 3-4N since the previous day); after two minutes *c* aggressively displaced *b* and defended this "new" territory for the rest of that day as well as the next. No copulations were observed in territory 3-4S, in any of the eight days it was occupied by a male; four copulations were observed in territory 3-4N in the 23 days it was occupied by a male. Also in 1989, territorial male *m* moved spontaneously from territory V to territory IV (about 15 m away) aggressively displaced the previous resident and defended territory IV for one hour, returning afterwards to territory V. Male *m* occupied territory V four more days and later defended territory IV again on two days; this male was observed defending two other territories before defending territory V for the first time. One copulation was observed in the 31 days territory V was occupied; two copulations were observed in the 32 days territory IV was occupied. Finally, in 1990, territorial male 30*a* moved from territory E to territory F' (which was unoccupied), about 25 meters away, and defended it for one day. This male was observed again defending territory

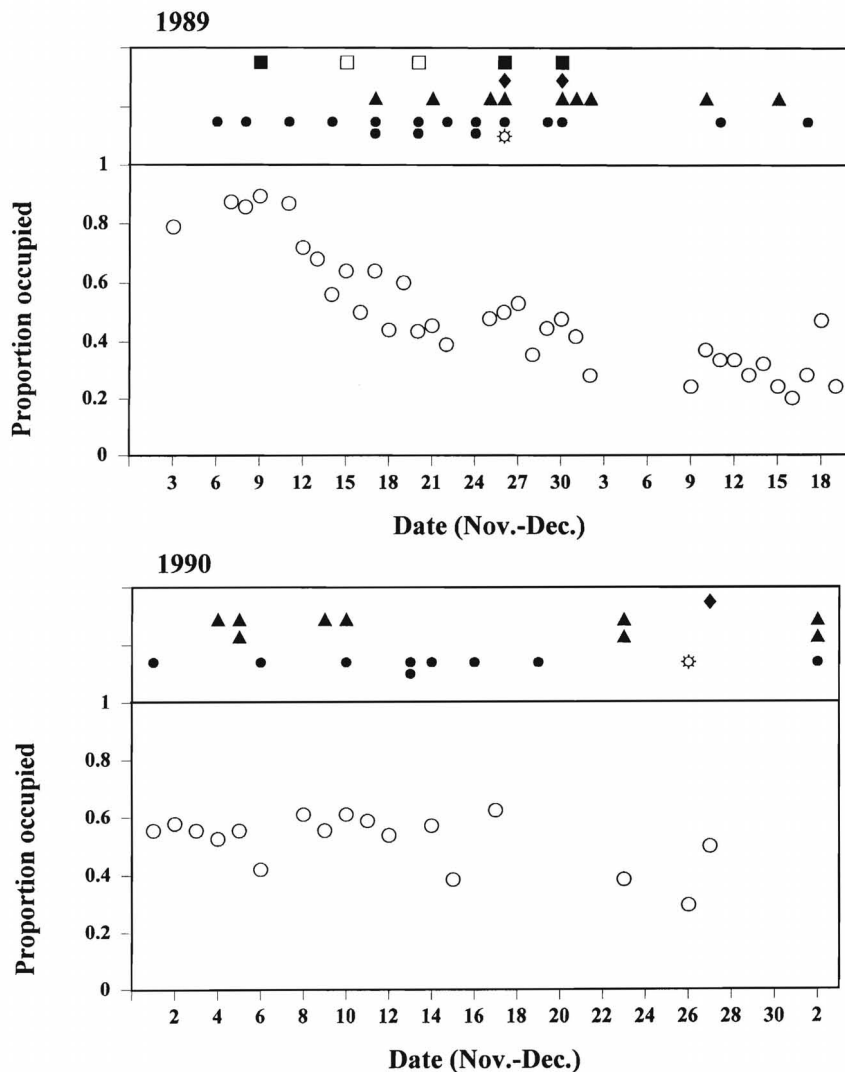


FIG. 1. Proportion of territories occupied by males, territory shifts and matings observed during the study periods of 1989 and 1990. In 1989, only those days in which 17 or more territories were surveyed are included; in 1990, only those in which 13 or more territories were surveyed are included. Key: *solid squares*: observed aggressive displacements; *empty squares*: suspected aggressive displacements; *diamonds*: spontaneous territory shifts; *triangles*: territory shifts due to unknown causes; *solid circles*: matings by monoterritorial males; *sunbursts*: matings by polyterritorial males; *empty circles*: proportion of territories occupied

TABLE 2. Summary of male characteristics. WL: wing length (cm). WW: wing wear category. L: longevity (days). T₁, T₂, T₃ and T₄ are, respectively, the number of days polyterritorial males defended their first, second, third and fourth territories. Cop: number of copulations.

	WL	WW	L	T ₁	T ₂	T ₃	T ₄	Cop
All males:								
mean ± SD	1.64 ± 0.1	1.56 ± 0.73	4.8 ± 5.4	2.4 ± 3	2 ± 2	2.7 ± 2.5	1.5 ± 0.7	0.15 ± 0.5
median	1.65	1	2	1	1	1	1.5	0
range	1.36–1.89	1–3	1–28	<1–14	<1–9	1–7	1–2	0–4
N	145	147	156	20	20	8	2	159
Males shifting via aggressive displacement:								
g'	1.62	3	7	4	<1	—	—	1
y	1.76	1	1	<1	1	—	—	0
Males shifting spontaneously:								
c	1.65	2	2	<1	2	—	—	0
m	1.55	1	17	1	1	5	2	0
30a	1.59	2	7	4	1	1	—	0

E on two days, four days after defending territory F'; afterwards he occupied territory A for one day. No copulations were observed in any of the six and four days territories E and F', respectively, were occupied. The fact that two spontaneous shifts were toward territories which apparently had higher copulation rates is in agreement with Prediction B2. The behavior of the last two males suggest sampling of territories, an idea implicit in Hypothesis B.

In agreement with Prediction B4, the two spontaneous territory shifts witnessed in 1989 occurred when male density was low (Fig. 1). In both years, spontaneous shifts were observed in the second half of the study period and after most of the copulations were observed (Fig. 1), suggesting that a decreasing encounter rate with females may be used by males as a cue for voluntarily leaving the territory.

Only two polyterritorial males were observed copulating, both in their second territory; these males were observed defending two territories and the causes of their territory shifts are unknown (one of these males was aggressively displaced from his second territory a few minutes after mating finished, and returned to his first territory).

DISCUSSION

In *Callophrys xami* some males shift territory because they are aggressively displaced from their territories by other males, or because they move spontaneously to a different territory. Given that the cause of 84% of the territory shifts detected was unknown, the relative importance of each of these causes cannot be determined.

The direct observations of aggressive displacement indicate that competition for territories is an important cause of shifts between territories. Rapid re-occupation of abandoned territories also suggests intense competition for territories. Competition happens in spite of the availability of unoccupied territories (Fig. 1), suggesting that competition varies in space at a local scale, probably in response to limited male movement and differences in territory quality, and, temporarily, due to local changes in male density and territory quality.

The existence of spontaneous territory shifts indicates that factors other than aggressiveness are responsible for some of the shifts. One possibility (Hypothesis B) is that males shift towards territories of higher quality (i.e., where mating rates are higher). We have insufficient data to test this possibility; however, the two observed copulations of polyterritorial males occurred in their second territories. Furthermore, two spontaneous shifts were towards territories where copulation rates seemed to be higher.

If the quality of prospective territories is difficult to determine for a male butterfly, males may simply tend to move to a different territory in

the hope of finding a better one. The time spent in a territory that is eventually abandoned may be necessary to determine its low quality or it may reflect a territory quality changing (decreasing) with time. Under these conditions we would expect to observe some cases of males shifting territory and returning to the previous one after some time, as was observed in two cases. Under this scenario, a smaller, and therefore more difficult to detect, difference between the average quality of pairs of territories sequentially occupied by males changing spontaneously might be expected. Intensive studies are needed to analyze the possible effects of territory characteristics on territory shifts.

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