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BEHAVIORAL ECOLOGY OF *LIBELLULA LUCTUOSA* (BURMEISTER) (ANISOPTERA: LIBELLULIDAE). 2. PROPOSED FUNCTIONS FOR TERRITORIAL BEHAVIORS

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A common North American pond dragonfly was studied in order to quantify the behavior of territorial individuals. This sp. has 5 distinct territorial behaviors: perching, patrolling, interspecific chasing, chasing adjacent territorial conspecifics, and chasing nonterritorial conspecifics. Associations between different territorial behaviors were established using sequential analysis of two-act sequences. After leaving a perch, males showed no significant tendency to engage preferentially in any of the other behaviors. However, after chasing other individuals, males preferentially patrolled; after patrolling, males typically perched. These results are interpreted in light of the proposed functions for territorial behaviors in *L. luctuosa*.

INTRODUCTION

Territoriality and the behavioral patterns associated with it are well studied in dragonflies, particularly in the Libellulidae (reviewed by PARR, 1983a). However, relatively few studies have attempted to investigate quantitatively the details of behavioral acts involved in territoriality other than to note gross differences between perching and flying (CAMPANELLA, 1975; HILTON, 1984; but see PARR & PARR, 1974; PARR, 1980, 1983b; HILDER & COLGAN, 1985; MOORE, 1987). Although the form of territorial behavior is similar for many dragonflies (CORBET, 1980; PARR, 1983a, 1983b), the purpose of these behaviors is less well known. The goal of this paper is to develop functional explanations for the detailed behavioral acts performed by territorial males. To this end, sequential analysis of two-act sequences (BAKEMAN &

GOTTMAN, 1986) is used to determine significant transitions between territorial behaviors in *Libellula luctuosa.*

Territoriality, as defined for dragonflies by "defense of a given area" (CORBET, 1962; PARR, 1983a) most often serves to provide males access to sexually active females and to provide females a predictable location for reproductive males (CORBET 1962, 1980; Parr, 1983a). Territories are typically located near bodies of water (CORBET, 1980; PARR, 1983a). Behavioral acts associated with territoriality are of two major types — perching and flying (CORBET, 1962; 1980; MAY, 1976; PARR, 1983a). Flying can be further divided into sexual, feeding, patrolling, and agonistic behavior (CORBET, 1980; PARR, 1983a).

Libellula luctuosa is a common North American dragonfly east of the Rocky Mountains (WALKER & CORBET, 1975) and is relatively unstudied. Only CAMPANELLA (1972, 1975) has explicitly examined the territorial behavior of this species. Territories in this species are established adjacent to, and over, small, permanent ponds (WALKER & CORBET, 1975). Male territorial behavior includes perching, aggression and patrolling, but does not include feeding (CAMPANELLA, 1972; MOORE, 1987). Sexual behavior is also excluded as a form of territorial behavior for this species as matings and mate guarding often occur over the center of the pond, away from male territories (MOORE, 1987).

METHODS

A complete description of methods and details of the territorial behaviors observed (see below) is given in MOORE (1987). Here, I briefly outline the major issues pertinent to this study.

L. luctuosa was studied in Boulder, CO, U.S.A. on a single small pond at an elevation of approximately 1580 m. Observations were made using focal observations (ALTMANN, 1974) on individually recognizable males from June 20 to August 14, 1985 between the hours of 1100 and 1430 when males were maximally active. Temperatures ranged from 26° to 30° C.

The occurrence and sequence of five different behaviors performed by territorial males were recorded; perching, patrolling, interspecific chases, territorial chases (chases between adjacent territorial males), and intruder chases (chases between non territorial conspecifics). Each of these behaviors is readily distinguishable by sight (see MOORE, 1987). Fifty-two males were observed for at least 10 min each (max. 14 min). The sequences of behavioral acts were analyzed for possible significant associations (conditional probabilities) between pairs of behaviors using methods outlined by BAKEMAN & GOTTMAN (1986). This procedure tests for significance of the transitional probabilities given the underlying distribution (i.e. frequency of occurrence) of the two-act sequences. Therefore, significance indicates that a particular transitional probability occurred more often than expected if two-act sequences were occurring at random. 2493 two-act sequences were analyzed; there are 20 different possible combinations of behaviors. In this analysis, transitions between the same actions did not occur as, by definition, a behavioral act could not follow itself.

RESULTS

The total number of occurrences of each behavior as the first or second act in

the two-event sequence is given in Table I. Patrolling was the most common behavior performed and accounted for 42% of the behaviors observed. Perching accounted for 32% of the behaviors, with territorial chases, intruder chases and interspecific chases occurring much less frequently.

Table I

The frequency of following behaviors given a specific starting behavior in two-act sequences in *Libellula luctuosa* (N=2493)

Preceding action	Following action					
	Perch	Patrol	Interspecific chase	Territorial chase	Intruder chase	*Total*
Perch	—	483	103	158	49	*793*
Patrol	707	—	17	233	85	*1042*
Interspecific chase	30	92	—	6	0	*128*
Territorial chase	19	363	0	—	7	*389*
Intruder chase	0	141	0	0	—	*141*
Total	*756*	*1079*	*120*	*397*	*141*	*2493*

Table II gives the observed conditional probabilities of the various behaviors occurring following a given first behavior. Significant differences in specific transitional probabilities were found for most of the behavioral acts. If a male was perching, intruder chases occurred significantly more often than expected, while all other acts did not occur significantly differently than the expected random distribution of following acts, given the observed frequency of each behavior. If a male was observed patrolling, perching occurred more often, while interspecific chases and territorial chases occurred less often than expected. Intruder chases did not differ from expected random occurrence. If a male was seen chasing an intruder, patrolling occurred more often and territorial and intruder chases occurred less often than expected as following acts. Following both territorial chases and intruder chases, patrolling occurred more often, while perching and others forms of chasing occurred less often than expected.

These results are also presented in Figure 1. For example, if a male was seen chasing an interspecific individual, 72% of the time the male followed this act with a patrol, while 23% of the time the male followed with a perch and only 5% of the time a male next performed a territorial chase. Following an intruder

Table II

The conditional probability of a particular two-act sequence and a test of significance for that transitional probability in *Libellula luctuosa*

First act (A)	Second act (B)	P(B/A)	Z-score*	Significance**
Perch	Patrol	0.61	-1.170	N.S.
,,	Interspecific chase	0.13	6.489	>
,,	Territorial chase	0.20	-2.013	N.S.
,,	Intruder chase	0.06	-2.082	N.S.
Patrol	Perch	0.68	10.363	>
,,	Interspecific chase	0.02	-7.156	<
,,	Territorial chase	0.22	-3.644	<
,,	Intruder chase	0.08	-1.859	N.S.
Interspecific chase	Perch	0.23	-2.154	N.S.
,,	Patrol	0.72	5.824	>
,,	Territorial chase	0.05	-3.567	<
,,	Intruder chase	0	-2.821	<
Territorial chase	Perch	0.05	-12.899	<
,,	Patrol	0.93	16.780	>
,,	Interspecific chase	0	-5.046	<
,,	Intruder chase	0.02	-3.914	<
Intruder chase	Perch	0	-8.390	<
,,	Patrol	1.00	13.251	>
,,	Interspecific chase	0	-2.806	<
,,	Territorial chase	0	-5.535	<

* Binomial test Z-score calculated using the formula

$$\frac{P(B/A) - P(B)}{\sqrt{\frac{P(B)\,[1-P(B)]}{N\,[P(A)]}}}$$

from BAKEMAN & GOTTMAN (1986)

** Assumes a significance level of 0.0025 using Bonferroni's correction to control for type I error. The symbol < indicates a two-act transition occurring less often than expected; > indicates a two-act transition occuring more often than expected; N.S. indicates no significant difference from the null hypothesis of a random distribution of following acts given a specific first act and the underlying frequencies of behavioral acts (see Tab. I).

chase, patrolling was seen 100% of the time. Following a territorial chase, patrolling was seen 93% of the time. The most common act following a perch was a patrol (61%), while the most common act following a patrol was a perch (68%).

DISCUSSION

Libellula luctuosa males perform five different behaviors on a territory. The majority of the time is spent by males perching (MOORE, 1987) and males leave their perch either to patrol, to chase interspecific dragonflies, to chase territorial males or to chase intruders. The frequency with which the various behaviors are seen is dependent on the population density of males (MOORE, 1987), although the percent of a time budget spent perching or flying was independent of the population density. It has been suggested that the fact that males adjust their flying behavior indicates a cost of flying in *L. luctuosa,* and males would be expected to budget the amount of time spent flying (MOORE, 1987). Territoriality is an important factor in the mating success of males in this species (CAMPANELLA, 1972, 1975; Moore, unpublished data). To the extent that the above behaviors are important in territoriality, males should spend their time on territories performing behaviors which are most likely to contribute either directly to mating success (i.e. chasing females) or indirectly to mating success (i.e. successfully defending and maintaining a territory).

The functions of the various male territorial behaviors can be in part predicted by the result of the male's behavior. The three chasing behaviors have the obvious and observable result of excluding other flying

males of this and other species from the male's defended area. It is therefore likely that these behavioral acts represent forms of aggression which function to maintain a territory. This idea is supported by sequential analysis: flying behavior in the form of chases occurs following any behavior except other chases. Obviously, chasing occurs in response to the presence of other dragonflies, not as a response to the preceding behavior. This may also be a function of male density in this species which, while variable, tends to be low so that only one male at a time ever invades a territory (MOORE, 1987).

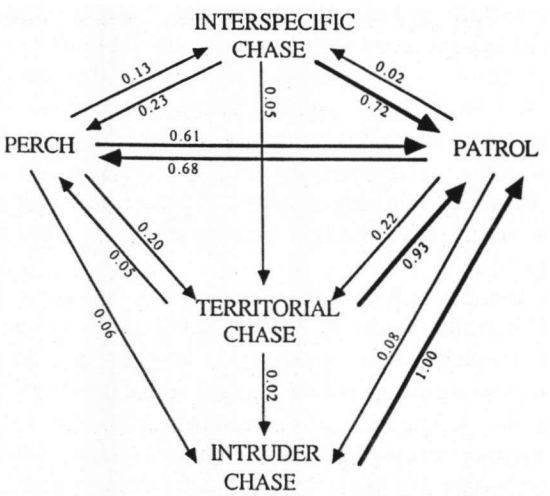

Fig. 1. The transitional probabilities of behavioral acts in territorial *Libellula luctuosa*. These two-act transitions represent the major behaviors performed by territorial males. The transitional probabilities are calculated based on focal observations of 52 males of at least 10 min. each. Males were scored for a particular act based on easily observed behaviors. Males were considered to be perching when they were not flying and were hanging onto reeds near the water edge. Patrolling was a slow, deliberate flight following the contours of the shoreline. Interspecific chases were similar to patrolling in appearance but made in response to the presence of a heterospecific. Territorial chases occurred between conspecific territorial males. Intruder chases occurred between a territorial male and a non territorial conspecific. The latter two acts were noticeably faster flying behaviors than patrolling or interspecific chases. See MOORE (1987) for a more complete description of the individual behavioral acts.

The other two behaviors, perching and patrolling, are not as easily interpreted. Perching may function to establish the fact that a territory is occupied, to conserve energy, or to prepare metabolically for flying (MAY, 1976; HEINRICH & CASEY, 1978). In any case, this act is unlikely to be the only behavior important in maintaining territorial possession, as nonterritorial males (satellite males) and females also perch on areas used as territories (MOORE, 1987). Patrolling is a more difficult act with which to deal. It does not occur in response to a specific stimulus, nor does it result in a specific outcome (MOORE, 1987). As a first step in understanding the meaning of patrolling, one can examine the interactions between this behavior and the others. If two acts are occurring together more frequently than expected, this should give some insight into how the act functions (BAKEMAN & GOTTMAN, 1986). PARR (1983a, 1983b)

predicts that patrolling functions as a mechanism of establishing the distribution of neighboring males. If this is the case, then patrolling should occur whenever a male returns after having left hie territory. My results support this idea. In fact, patrolling is the behavior performed most frequently following chases by the territorial male, almost to the exclusion of all other behaviors. Alternatively, patrolling may function as a mechanism to insure sole possession of a territory (i.e. determining the presence of intruders). If patrols insure possession, then one would expect to observe patrols occurring more frequently before chases. However, chasing occurred less frequently following patrols. Further evidence that patrolling is not performed to insure possession of a territory is that perching occurs more frequently then expected following a patrol. Rather, this result supports the idea that patrols occur as a transition between aggression and perching, at least in *L. luctuosa.*

In sum, it appears that in *L. luctuosa* territories are maintained by aggression through chasing. Perching and patrolling occur as a consequence and not as a cause of defending a territory. Perching allows males to (1) be in position to exclude other males, (2) be in position to encounter females, and (3) become metabolically ready to fly. Patrolling functions as a transition from aggression to perching. It may also be used to gather information about neighbors, such as their presence, position, and current behavior, but this is more difficult to demonstrate.

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