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Territorial Conflicts in Males of the Dragonfly, *Orthetrum japonicum japonicum* (Odonata: Libellulidae): The Role of Body Size

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ABSTRACT—The relationship between body size and the results of territorial conflicts was studied in males of the dragonfly, *Orthetrum japonicum japonicum*. Territorial residents were larger than intruders in body width, but not in hind wing length. Winners of territorial conflicts were larger than losers in body width, but not in hind wing length. This difference was attributed to the fact that residents were larger than intruders. The results of territorial conflicts were more strongly affected by the role of the opponents (resident or intruder) than by the difference in their body sizes. Territorial males arrived at the territorial sites earlier than non-territorial ones on a given day. The body size of males arriving at the study area earlier in a day was not larger than that of males arriving later.

INTRODUCTION

It is widely accepted that the difference in the body size of opponents is one of major factors governing results of animal conflicts (e.g., Howard, 1978; Maynard Smith, 1982). Males of dragonflies and damselflies (odonates) often show territorial behavior (Corbet, 1980). The role of body size in territorial conflicts in odonates has been examined in several studies (Miller, 1983; Fincke, 1984; Tsubaki and Ono, 1987; Kasuya *et al.*, 1987; reviewed by Higashi *et al.*, 1987). These studies reported only that body size of territorial males was larger than that of non-territorial ones (the study of Tsubaki and Ono (1987) is an exception; see also Higashi *et al.*, 1987). This difference can be a consequence of the superiority of larger males in territorial conflicts, or the by-product of other factors that are correlated with body size and territorial residence. Tsubaki and Ubukata (in Higashi *et al.*, 1987) suggested that the effect of a difference in fighting ability between opponents is stronger than that of territorial residence (residence or intruder) in territorial conflicts of male odonates.

Recently, reproductive success and selection have been measured in several species of odonates (McVey, 1988; Fincke, 1986; Koenig and Albano, 1987; Anholt, 1991). Studies on the significance of body size in territorial conflicts of odonates can provide essential information on the interpretation of selection patterns on morphological characters. In the present study, we present data on the territorial conflicts of males of the dragonfly, *Orthetrum japonicum japonicum* (Uhler) (Odonata: Libellulidae) and analyze the relationship between measures of body size and the results of conflicts. We also analyze the relationship between the results of conflicts and other possible correlates. Results of measurement of the reproductive success and selection on morphological characters in the same population will be reported elsewhere.

MATERIALS AND METHODS

Observations of the reproductive behavior of *O. japonicum japonicum* were made in a weakly undulating terrain near small pools and streams in Touzima, Maki, Niigata Prefecture, Japan (Fig. 1), from May 13 to May 22 , 1986. Because the reproductive behavior of a population of *O. japonicum japonicum* occurs in a short period in spring, the above period covered most of mating of this dragonfly in the study area in that year.

O. japonicum japonicum males defended territories over a water surface. Males copulated with receptive females which flew to these territorial sites for oviposition. Males arrived at the study area in the morning of sunny or slightly cloudy days and left the study area for hills surrounding the study area in the afternoon or evening. The whole sequence of reproductive behavior (from pre-copulatory tandem flight to oviposition) was usually observed in the territorial sites where males copulated with females. The observations were made from 8:00 to 16:00. Adults were caught with a hand-held net and marked individually with a combination of dots of paint on their wings for later identification. We did not estimate age of adults from body status (soft or hard, color etc.) because the reproductive period was very short and estimation of age from the status of body with high resolution was not possible for most adults in the present study.

A territorial conflict usually occurred between two males in the air. When a single territorial conflict was involved at a territorial site, the male at the site before the conflict is referred to as the resident and the later-arriving opponent is referred to as the intruder. A male 'wins' when it returns to the territorial site earlier than the other

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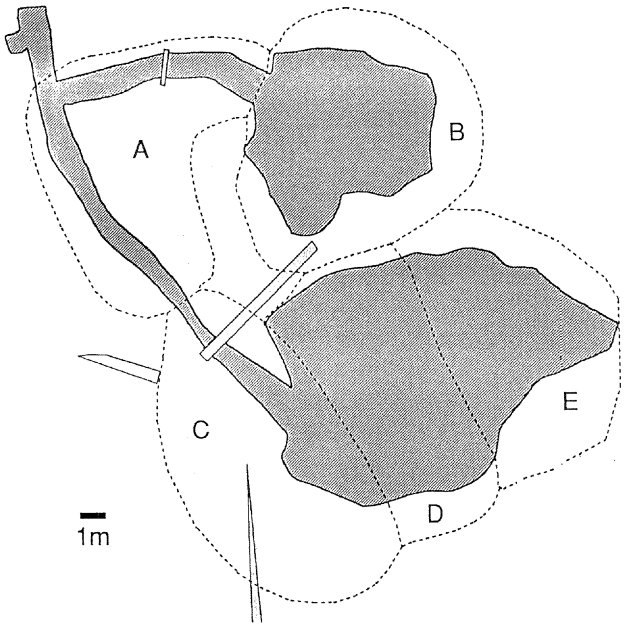

Fig. 1. Study area. Hatched area, water surface; broken line, range of territorial site; A-E, territorial sites; spotted area, fallen tree.

opponent. Here, we refer to resident and intruder as roles of the opponents. An intruder had either established a territorial residence at another site before the conflict, or it was a non-territorial floater. Two observers ascertained the establishment of territorial residence by observations of perching behavior and chasing behavior against other males that intruded into the territorial site. The observers were able to record territorial behavior, results of conflicts and identity of opponents without field glasses. Territorial residence of a male at a given site usually lasted for hours. Males that had territorial residence at any site in a day were referred to as territorial males while males that did not have territorial residence at any site in a day were referred to as non-territorial males.

Body width (the largest width of the thorax in dorsal view) and wing length (from the apex to the hind wing base) were measured with a slide caliper to the nearest 0.1 mm. Both measurements are indicative of the body size. Preliminary observations showed that these two characters were important in reproductive behavior in the study area. The measures are expressed in 0.1-mm units (e.g., 1 mm = 10 units) if not otherwise mentioned.

RESULTS

Table 1 shows the results of territorial conflicts between territorial residents and non-territorial males, i.e., conflicts in which the intruder was a territorial resident of a neighboring site were excluded. Thus, the table shows the results of the conflicts between territorial residents and non-territorial males. Territorial conflicts usually occurred as pairwise contests between a resident and an intruder as noted in Materials and Methods. In some cases, three or more males (one resident and two or more intruders) were involved in a conflict. Such cases were not included in the analysis in the present study. We count only the first conflict between a given pair (and roles) of males during an uninterrupted occupation of the territorial site by a territorial resident to avoid pseudo-replication.

Table 1. Body size and results of territorial conflicts

(a) body width

	resident > intruder	resident = intruder	resident < intruder
resident wins	30	0	13
intruder wins	2	0	0

(b) wing length

	resident > intruder	resident = intruder	resident < intruder
resident wins	24	0	19
intruder wins	1	0	1

Residents won significantly more frequently (43/45 = 95.6%) than intruders ($\chi^2 = 37.35$, df = 1, $P < 0.001$). The data in Table 1 show that the residents were significantly larger than intruders in body width ($\chi^2 = 8.02$, df = 1, $P < 0.01$), but not significantly larger in wing length ($\chi^2 = 0.56$, df = 1, $P > 0.3$).

Territorial males on a given day were significantly larger than non- territorial males in body width ($z = 1.963$, $P < 0.05$). However, the difference in wing length was not significant ($z = 0.60$, $P > 0.5$) (two-sample matched set test; Meddis, 1984) (Fig. 2). Territorial males on a given day were also territorial on the following day in significantly higher proportion (96.3%) than were non-territorial male on the following day (12.5%) (two-sample test for multiple frequency tables, $z = 5.55$, $P < 0.001$; Meddis, 1984).

Next, we analyzed the relationship between the difference in body size and the results of territorial conflicts. For body width, larger males won significantly more conflicts than smaller ones ($\chi^2 = 5.23$, df = 1, $P < 0.05$). For wing length, larger males did not win significantly more conflicts than smaller ones ($\chi^2 = 0.56$, df = 1, $P > 0.3$).

The superiority of males with larger body width in territorial conflicts can be either a consequence of the difference in body width itself or a consequence of another factor that is correlated with the difference in body width. Residents did not win more frequently when they were larger than intruders than when they were smaller than intruders, for both measures of body size (Fisher's exact probability test, $P = 0.76$ for body width, and $P = 0.44$ for wing length). Whether the role of an opponent (resident or intruder) affects the relationship between body size and the proportion of wins can be answered with the data of Table 1. For both measures of body size, larger males won more when they were residents than when they were intruders ($\chi^2 = 37.26$, df = 1, $P < 0.001$ for wing length and Fisher's exact probability test, $P = 6.95 \times 10^{-10}$ for body width). The

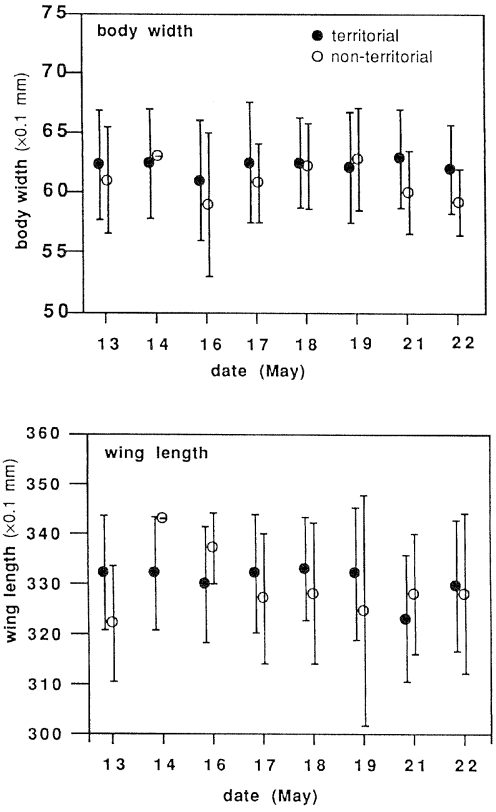

Fig. 2. Body sizes of territorial and non-territorial males on each day of observation. Dots, mean of territorial males; open circles, mean of non-territorial males. Bar, SD.

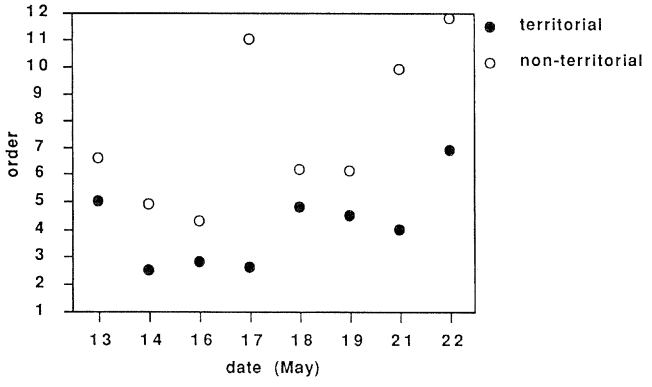

Fig. 3. Relationship between the order of arrival at the study area and territorial residence on each day. Dots, mean order of territorial males; open circles, mean order of non-territorial males.

results of the two kinds of tests show that residence is more important than larger body size in deciding the outcome of a conflict.

Figure 3 shows the relationship between the order of arrival at the study area and territorial residence on each day. Smaller values of order show that males arrived at the study area earlier in the morning than did other males on a given day. On each day, territorial males arrived at the study area significantly earlier than did non-territorial males (Fisher's

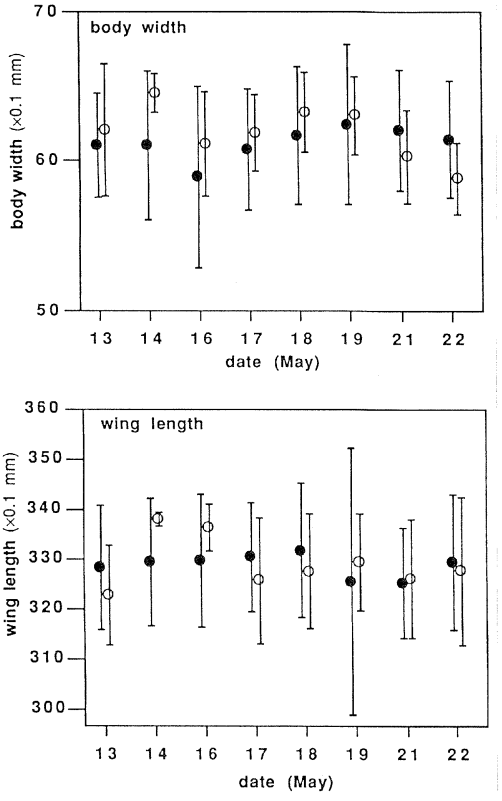

Fig. 4. Body size of males arriving at the study area earlier and later in the day. Dots, mean of early arriving males; open circles, mean of later arriving males. Bar, SD.

permutation test for paired sample, P = 0.0088). Males arriving at the study area in a given day were divided into two groups: the early arriving half and the late arriving half (when the total number of males was odd, the middle arriving male was put in the early group). The body size of early arriving males was not significantly larger than that of late arriving males (Fig. 4; z = 0.050 for body width and z = 0.966 for wing length, P > 0.3, two-sample matched set test; Meddis, 1984).

DISCUSSION

In the population of *O. japonicum japonicum* in the present study, there was a strong positive correlation between the duration of territorial residence of a male and its mating success (r = 0.856, Kasuya *et al.*, in preparation). Thus, an analysis of the factors governing the results of territorial conflicts can be important for the study of the evolution of territorial and mating behavior.

The body width of territorial residents was larger than those of intruders (Table 1). This result can be interpreted in two ways. The first hypothesis is that a male with a larger body width is stronger in territorial conflicts than a male with a smaller body size. The second hypothesis is that this higher proportion of wins of a male with larger body size is a by-product of another factor that is correlated with body size. The first hypothesis assumes a direct causal relationship between

the difference in body size and the result of territorial conflicts. The second one assumes that there is not such a relationship between body size and the result of territorial conflicts and that the observed relationship between body size and the result of conflicts is a by-product of a true causal relationship.

The first hypothesis predicts that the difference in body size between residents and intruders affects the results of territorial conflicts when the role (resident or intruder) of opponents is fixed. This prediction is inconsistent with the data of Table 1. Residents did not win more when they were larger than intruders than when they were smaller than intruders, for both measures of body size.

Analyses of the data in Table 1 show that one of the factors that affects the results of territorial conflicts is the role of opponents in territorial conflicts (resident/intruder). The role of opponents (resident or intruder) affects the relationship between body size and the proportion of wins, while the difference in the body size of opponents does not affect the relationship between the role of opponents and the proportion of wins. If the body size of a male represents its fighting ability, the present result is contrary to the hypothesis of Tsubaki and Ubukata (in Higashi *et al.*, 1987) that the effect of the difference in fighting ability on the results of territorial conflicts in odonates is stronger than that of the role of opponents. However, fighting ability may depend on factors other than the body size of males (e.g., age of males) as suggested by Tsubaki and Ubukata.

The relationship between body size and the proportion of wins observed in this study is thus a by-product of the relationship between body size and the role of opponents. In other words, the observed relationship between body size and the proportion of wins is due to the facts that the resident wins more and that the body widths of residents were larger than those of intruders. Because the present data are consistent with the second hypothesis, it is natural to assume that the residents were larger than intruders because the larger males arrived at the study area earlier than smaller males on each day of a reproductive period. Body size is considered to be functionally related to thermoregulatory ability (Corbet, 1980). If a measure of body size is correlated with the ability to thermoregulate, we expect that larger (or smaller) males would arrive at the reproductive area earlier in the morning and that they would be territorial. This possibility can be tested by examining the relationship between the order of arrival at the study area and body size and the relationship between the order of arrival and territorial residence. Though the territorial males arrived earlier (Fig. 3), Fig. 4 shows that males arriving earlier are not larger than males arriving later in either measure of body size. This result is inconsistent with the hypothesis that the larger males arrive at the study area earlier than smaller males on each day.

Thus, another factor should be responsible for the difference in body size between residents and intruders. In this population, males are territorial on consecutive days even though territories were abandoned and regained every day. This suggests the importance of learning or memory of past conflicts (e.g., Maynard Smith, 1982) in territorial residence. Causal factors that are responsible for larger males being territorial residents more frequently can be elucidated in future studies, especially field experiments in which territorial males of known properties are artificially replaced with other males.

Our results are different from those of Tsubaki and Ono (1987), who studied in detail the effect of body size on territorial residence in *Nannophya pygmaea*. In *N. pygmaea*, body size (forewing length) played an important role in territorial conflicts between males and was correlated with copulation success. The length of the reproductive period of a population is very different between these two species. It was 4 months in *N. pygmaea* (Tsubaki and Ono, 1987) but only about two weeks in the *O. japonicum japonicum* population in this study. This may explain the difference since the variation in age among the adult males at a given time could be small in *O. japonicum japonicum*. Further studies in various species can elucidate the factors governing the results of territorial conflicts. Factors including age of males and fat reserve can be important (Campanella and Wolf, 1974; Marden and Waage, 1990).

The results of the present study suggest that the sizes of different body parts have different roles. The dragonflies cannot be described by a single body size; rather the lengths (or weights) of various parts of the body are needed. Use of a single morphological character to represent body size can be misleading (Arnold and Wade, 1984).

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