Behavior of Males in a Reproductive Aggregation of the Banded Demoiselle *Calopteryx splendens* (Insecta, Odonata)

E. N. Panov and A. S. Opaev

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia
e-mail: panoven@mail.ru

Abstract—The view according to which damselfly males practice two alternative reproductive tactics of access to females is critically discussed. It is widely accepted that some males ("territorial" ones) have priority as potential female partners, while others ("sneakers" or "wanderers") are incapable of retaining an individual territory. They have a chance of mating only by intruding briefly into the area defended by a "territorial" male when a female is present there. Thus, the tactics of a "territorial" male consists in waiting for a female in its territory and copulating with it "by agreement," whereas non-territorial males resort to forced copulations. By observation of individually marked males (48 out of 118) it was shown that every male could be regarded as "territorial" during a certain period and as a "wanderer" before and after it. Thus, no correlation between the modes of space use by a male (residence/mobility) and the characters of its external morphology and/or signal behavior appears to be possible in principle. According to the data obtained, a more plausible explanation is that the female chooses not the male but the best area for oviposition. In addition, it was ascertained that adherence to forced copulations cannot constitute successful "tactics" since they rarely result in insemination, neither by "territorial" nor "non-territorial" males. In other words, we are dealing not with certain alternative tactics (i.e., specialized adaptive mechanisms that have evolved in the species) but simply with the results of different sets of circumstances at a given moment.

DOI: 10.1134/S0013873813070014

In the modern model of animal social behavior, the latter is commonly considered as a conglomerate of more or less autonomous fragments, each of them being a priori ascribed its own specific function and, consequently, its own independent evolutionary history (Gould and Lewontin, 1979). One of the examples of such an approach may be the widespread idea of the so-called **alternative** tactics of the male reproductive behavior. According to these views, each population includes some "territorial" males, which enjoy priority in producing offspring, and some males that are unable to retain an individual territory. The latter manage to mate only by seizing an opportunity and invading, for a brief moment, the area occupied by a territorial male. They are referred to as "non-territorial males," or "sneakers."

There are numerous examples of this dichotomy being applied to different species from all the classes of vertebrates (fishes, amphibians, reptiles, and birds). A search for "male alternative tactics" in the Internet yields 11 300 000 literary sources. Recently, this dichotomy was borrowed from vertebrate ethology into the field of studying social relations in insect populations. However, some students of behavior of calopterygid damselflies consider this subdivision of males into "territorial" and "non-territorial" to be artificial, suggesting that a particular mode of their spatial behavior may instead be conditioned by transitory circumstances (see, for example, Forsyth and Montgomerie, 1987; Koskimäki et al., 2009).

The goal of the present paper is to demonstrate the invalidity of this approach (see its criticism in Panov, 2009), both in general and in application to the reproductive aggregations of demoiselles of the genus *Calopteryx*. In our opinion, the socio-sexual relations observed in such populations are not necessarily shaped by certain specialized determinants responsible for the male reproductive behavior. Instead, they represent one of the ways of realization of a broad, though not at all limitless, range of behavioral potentials of the species, which is determined by momentary conditions (transient changes in ecological conditions, the socio-demographic structure of the assemblage, the age of the male, and many others). In other words, we are dealing not with a specialized adaptive mechanism developed by the species in the course of its evolution but simply with the result of a certain set of circumstances at a given moment.

MATERIALS AND METHODS

The Object of Study, Materials, and Methods

Systematic observations of the behavior of the banded demoiselle (*Calopteryx splendens*) were carried out from June 12 to July 27, 2010 along a 20-m segment of the river Tyumba in Vladimir Province (the environs of Mstera). The distribution of these damselflies in their favorite habitats was not uniform. Although they could be observed in all the localities with running water and aquatic vegetation providing perches for males and oviposition sites for females, rather dense aggregations were formed in certain places. Sometimes up to 50–70 active males could be counted along a 15-m segment of the stream.

The general picture of the events happening in such aggregations was given in a previous communication (Panov and Pavlova, 2009). The reproductive aggregations of damselflies were compared there with leks of birds. The common feature is that both are organized as a mosaic of individual territories of males which are visited by females ready for copulation. The main feature distinguishing damselfly aggregations from bird leks is that territories inhabited by females are not separated from the area of male aggregation but widely overlap with the latter. Moreover, females which are not ready for mating occur within the mosaic of male territories and feed there in the morning and evening time without experiencing any mating attempts on the part of males. In such periods, females keep to the tops of semiaquatic vegetation, at a height of about 1 m. There, such females, as well as sexually inactive males (see below), are virtually excluded from the social relations which develop close to the water surface, on the lower fragments of semiaquatic vegetation and on the submerged ones.

Our work was mostly carried out within a riverside plot of about 100 m^2, where the dynamic density of males was approximately 50 ind. at the height of the mating season. Within the period between June 15 and July 20, 118 males and 32 females were individually marked. Observations were also carried out in July 21–24 in another plot which differed from the main one in denser aquatic vegetation; 8 more males were marked there.

The marks were put on different parts of the damselfly bodies using a mixture of oil-paint and colorless nail varnish. Having used nearly all of the relatively simple mark combinations (such as red dorsum—red

abdomen base—red abdomen tip), we started putting marks on the wings with a white or red marker. These methods, unlike the traditional ones (putting numbers on the wings), allowed individual damselflies to be identified even in flight. After marking, the damselflies were photographed with their wings fixed on a scaled pad with a medical elastic band, for subsequent measurement in the laboratory.

The observation data were mainly preserved by video recording. Since the goal of our work was to analyze the usually transient interrelations between individuals, we mainly used the method of continuous recording of the behavior of certain males. Only in this way it was possible to record the whole sequence of events, from the appearance of a female in the male's territory to the moment of copulation. Due to the rarity of this event, only 20 copulations could be recorded even with the use of this method. The observation data were also preserved using a voice recorder.

In June 12–24, everything that was happening in the main study plot (conflicts between males, copulations, and appearance of previously marked individuals) was simultaneously recorded from two different points by two observers equipped with Sony CCD-TR570E and CCD-TR3400E camcorders, binoculars, and cameras. The total time of observation was about 80 man-hours. The video records on 22 cassettes are kept at the Laboratory for Comparative Behavior and Biocommunication of Severtsov Institute of Ecology and Evolution.

On Two Male Reproductive "Tactics" in the Banded Demoiselle

The a priori subdivision of males of the genus *Calopteryx* into "territorial" and "non-territorial" has been dominant in the literature since the publication of Pajunen (1966). Repeated attempts have been made to fortify this idea by asserting that differences between the two groups manifest themselves not only in the behavior of males but also in their external morphological characters; in particular, non-territorial males were believed to be less brightly colored (see, e.g., Grether, 1997; Siva-Jothy, 1999). In the latter of the cited papers it was assumed that females of *C. splendens xanthostoma* could distinguish the different levels of male wing pigmentation (Fig. 1) before mating. On the other hand, a meticulous study of *Calopteryx maculata*, using precise spectrometric measurements, could not reveal any differences in external morphology between the males considered to be "terri-
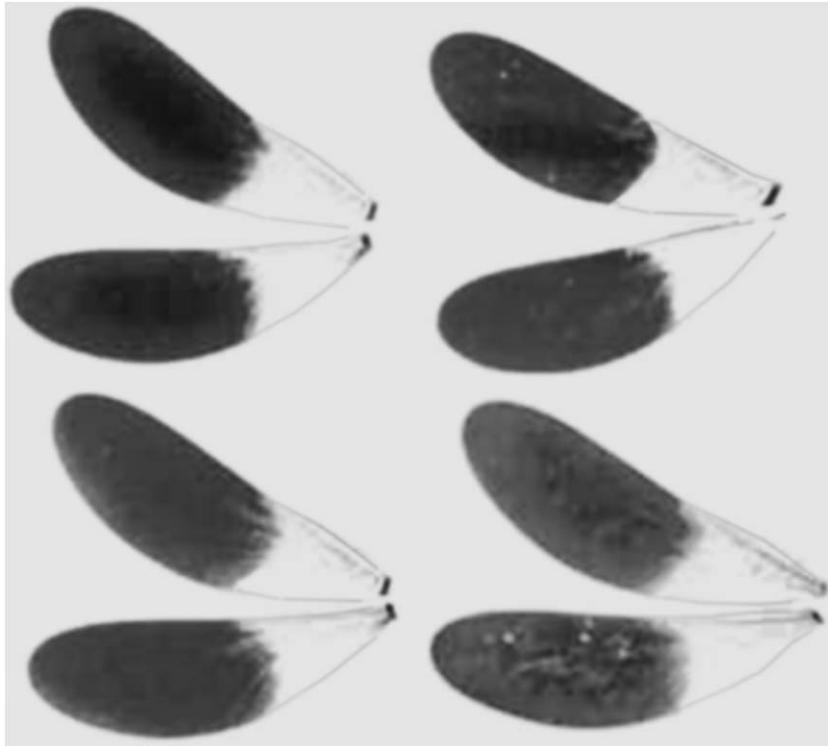
Fig. 1. Variability of the degree of wing pigmentation in males of *C. splendens xanthostoma* (after Siva-Jothy, 1999).

torial" and "non-territorial" (Shorter, 2007). Neither was it possible to show such differences in our material.

Our data suggest that the very scheme of subdividing the males into the two above categories has no sufficient ground. The term "territoriality" means nothing more than the stable presence of a male within the limits of the territory where it is visited by females ready for mating. However, such behavior is characteristic of only one of the stages in the male's biography. This means that any particular male may be considered as "territorial" at one time and "non-territorial" at another. It is therefore quite obvious that no correlation can be revealed between the ways of space use by the male (residency/mobility) and any characters of its external morphology.

Further, there is no direct connection between this dichotomy (residency/mobility) and the mode of behavior of males toward females. It is generally believed that the behavior of the "territorial" males is limited to waiting for females in their respective territories and copulations with the "willing" mates, whereas the "non-territorial" males, or sneakers, resort to the so-called forced copulations. In reality, this is not so, since any male appears to be ready for forced copulation if it has a good opportunity to do it. Such

a situation arises, in particular, if after laying eggs under water, the female surfaces within the territory of a male other than the one which copulated with her before.

Besides, adherence to forced copulation by itself cannot be regarded as successful "tactics" since such forced contacts never result in insemination. Neither "territorial" nor "non-territorial" males achieve success in this case. This view is supported by the data on the behavior of individually marked damselfly males presented below. Of 118 marked males, 48 (40.7%) were encountered for the second time with intervals varying from 1 to 19 days (the mean value is 5.5 ± 3.9; see Table 1).

RESULTS

The General Scheme of Behavior of Males and Their Competitive Interaction

The spatial distribution of males. Males spent the night in dense riverside vegetation, forming compact aggregations with the minimum individual distances of only several centimeters. As the air began to warm up, they spread along the river perching on stems and leaves of plants. The sexually active males occupied perches situated not higher than 20–25 cm from the

Table 1. The fates of individually marked *C. splendens* males

Parameter	$X \pm SD$ (median)	Range	Number of males
Number of days between the capture and the last record	5.5 ± 3.9 (5)	1–19	48
Number of consecutive days during which the male was recorded daily	1.5 ± 0.9 (1)	1–4	46
Number of days between the first and the last records	1.8 ± 1.2 (1)	1–7	46

water surface. Only they were visited by females ready for copulation, whereas sexually inactive ones kept to the upper layers of vegetation, where they were usually ignored by the male "owning" the perch. Wandering males, which were sexually inactive at that moment, also perched high above the water surface.

Males ready for copulation were non-uniformly distributed within the reproductive aggregation, depending on the arrangement of convenient perches. In the study plot shown in Fig. 2, the perches were provided by the lower stem leaves of the flowering rush *Butomus umbellatus*. As can be seen from the scheme, individual perches of neighboring males were sometimes positioned slightly more than 1 m apart, maximally up to 4–5 m. From Fig. 2 it also follows that perches were not equally attractive for males; they could be subdivided into three categories. Perches of two categories were used by sexually active males permanently or from time to time, whereas perches of the third category were used by sexually inactive males. In the course of the reproduction season, males possessing the right to maximally preferred perches of the first category replaced one another in time with greater or lesser regularity. According to the marking data, the greatest period of a perch being owned by a male was 5 days (9 days, with a gap of 2 days).

One gains an impression that actually it is for such perches and not for the territory as such that males competed. As it will be shown below, the degree of stability in the male using its favorite perch makes it possible to predict reliably the subsequent fate of the male as the owner of the given territory.

The structure of the individual territory and the mode of its use by the male. Such a perch was the main component of the male's individual territory and, thus, the center of its activity. Together with the neighboring fragments of the lower vegetation layer, it formed the core area of the territory whose borders were completely diffuse. Therefore, we prefer the term "individual area" to "territory," even though the latter is commonly used in the literature on these damselflies. This decision is also supported by the fact that the male's behavior aimed at keeping the individual area does not quite correspond to the true territorial behavior (see below).

During the period when the male exclusively owned a certain area, he spent most of the time on its main perch though it might occasionally use 2–3 others located within a radius of 1.5–2 m. The male did not stay motionless for a long time; he regularly flew up and immediately returned to the same preferred perch
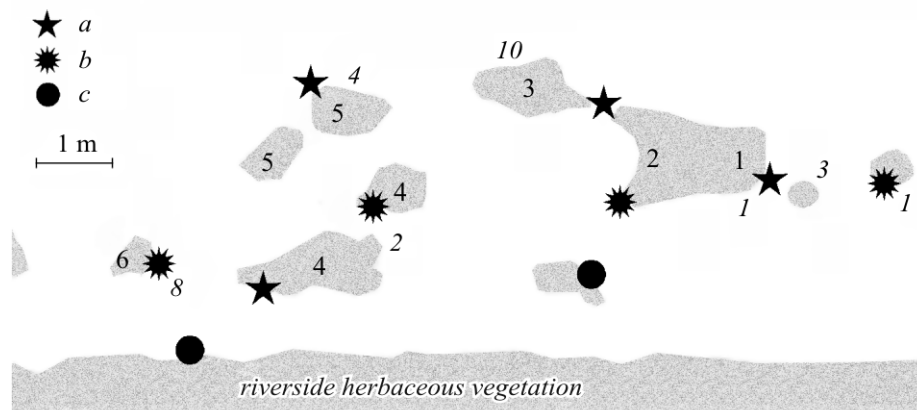

Fig. 2. The scheme of the observation plot. The number of copulations recorded on each perch is indicated. Perches: *a*, persistently occupied by males; *b*, those occupied only from time to time; *c*, used by males which do not compete with others for the most preferred perches. For other designations, see text.

or to another one located nearby. Such flights could be subdivided into 1) spontaneous and 2) those triggered by the appearance of another male (more rarely, female) in the given area.

One timing set out of many obtained in this research is given below as an example. Uninterrupted observation of a marked male during 4 h showed that it flew up 274 times; 232 of these flights were spontaneous and only 42 (15.3%) were triggered. After leaving its "main" perch, the male returned to it 131 times (47.8%). The duration of spontaneous flights varied from 0.5 to 12 s, with the mean value being only 2.52 ± 2.16 s, and the median, 2 s ($n = 45$).

As for triggered flights, for quite obvious reasons they were much longer, varying from 3 to 33 s (the mean being 10.02 ± 7.91 s, the median, 7 s, $n = 42$). Their duration was greater due to the fact that most of such flights resulted in a short contact with an invading male (less frequently, in an attempt to approach a female without leaving the individual area).

However, it is essential that during the period of stable association with his area, the male avoided prolonged needless contacts with other males. The regular spontaneous take-offs from the main perch were usually followed by very quick (within the first seconds) landings on the same perch. The same could be observed when the flight was triggered by another male passing through the area. During this period of stable association with his area, the male often ignored other males flying by and did not fly up at all at their approach. Neither did he take part in the conflicts of males occupying adjoining areas. The male at this stage appeared to follow an autonomous program of "staying on the perch if possible."

The following observations showed the pattern of spontaneous flights to be somehow associated with the social status and reproductive potential of the male. As soon as the pretender managed to drive out the former owner of a given area, he immediately started a sequence of spontaneous flights whereas the number of triggered flights decreased. In other words, the above-mentioned autonomous program of "staying on the perch if possible" was put into action. On the other hand, spontaneous flights were observed noticeably less frequently in males which left their areas on their own account or were forced out to the periphery of the aggregation.

Agonistic behavior and change of the owner. We use the term "agonistic behavior" as one more suitable

for that observed in males of calopterygid damselflies, preferring it to the terms "territorial" and "aggressive behavior" which are used in the literature on these species[1]. As mentioned above, the male's individual area does not fit the strict definition of an "individual territory" as of a certain space distinctly outlined by the borders which are protected by its owner. Still more important is the fact that conflicts between males were devoid of evident signs of aggression. Direct contacts between males were observed only when one of them claimed the female which was being held by the other. At such moments the former male might grasp the head of the latter with its cerci (in the same way as he would grasp a female). However, this appeared as the result of pure chance rather than an intended contact aggression. In view of all the above, we consider the words "attack" and "fighting" widely used in the literature on calopterygid damselflies to be misleading.

The most common form of conflict between males was the so-called joint fluttering flight (see video in http://panov-ethology.ru/download/mothe-flight.avi). They were described in detail in the paper on the behavior of males of the beautiful demoiselle *C. virgo* (Pajunen, 1966). It should be emphasized that during such contacts which may last for tens of minutes, none of the participants attempted to shorten the individual distance which was maintained at about 10 cm. It was also impossible to reveal the role of the pursuer and the pursued, i.e., none of the males was driving, much less attacking, the other (for details, see Panov et al., 2010).

Neither these interactions nor much more intense ones referred to by us as "pursuits" (Panov et al., 2010) resulted by themselves in forcing out the owner of the area by the pretender. In such situations the following sequence of events was observed. The pretender demonstrated its intentions by the fact that already at the moment of its appearance it began to land persistently on the owner's main perch or in the immediate vicinity of it, clearly ignoring the response of the owner. The latter in this situation fluttered chaotically in the air trying over and over again to drive the newcomer from the contested perch. Another such episode was followed by a new series of joint fluttering flights or prolonged "pursuits." However, it is

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[1] The concepts of "territorial behavior" and "aggressive behavior" tend to be erroneously equated (see, e.g., Contreras- Gurduño et al., 2009).

most important that the owner of the area never landed on either its main perch or any other, even when they remained vacant. The pretender, on the contrary, landed on them at the least opportunity.

The conflict could be resolved within 1–1.5 hours. If the initial owner finally ventured to land on the contested main perch at least several times running, he had a good chance to retain its right to the area. The higher was the flying activity of the owner, the weaker was its chance. If the pretender landed on the perch again and again with its initial persistence, it won the contest and acquired the sole right to the given area. It should be noted that conflicts following this scheme could take many hours. The longer the confrontation lasted, the more probable became the change of the owner of the area.

All the data presented in this section allow one to suggest that at the initial stage of its sexual activity peak, the male chooses a convenient perch but not the area as such. Loss of a perch also means loss of an individual area.

The Dynamics of the Social Status of Males

It follows from the above that the mere fact of the male staying for a long time within a limited sector of space (which at first sight may be regarded as a characteristic of a "territorial" male) is not yet an indication of its reproductive potential at that time. Two factors are necessary to ensure his status as breeder: first, a sufficiently high level of motor activity estimated by the frequency of spontaneous flights; second, the presence around the male's perch of semi-submerged aquatic vegetation on which the female lays eggs immediately after copulation. As for the phenotypic traits of males, we did not find any support of the idea that the most successful males should be the largest (Table 2). Besides, males bearing white and red marks were successful in copulation, indicating that the female paid little attention to the details of the male's appearance but responded to its general movement pattern.

The following example supports the above view. Area 6 (Fig. 2) was owned for three days by a male marked as BX on 12.VII. In the evening hours of 14 and 15.VII, when this male was continuously observed, he made on average 58 spontaneous flights per hour. Six successful copulations and one capture of the female which did not result in insemination were recorded during these days. The attractiveness of this

particular area for females was indicated by the fact that on the second of these days, females chose it at 18.00, 18.18, 19.51, and 20.08. In the evening of 16.VII, the male increased his mobility gradually losing connection with its main perch, and on the next day its perch was vacant.

Within the period between 18 and 21.VII., male no. 96 could be periodically observed in the zone embracing area 6 and the left edge of area 4 (Fig. 2). It often used the main perch of BX male but almost never flew up spontaneously. In addition, the water level dropped during these days, so that vegetation which used to be only slightly exposed appeared well above the water surface and became unsuitable as an oviposition substrate. Therefore, it is not surprising that during these three days females did not visit this part of the experimental plot.

Thus, in our opinion, the dichotomy "a territorial/non-territorial male" should be replaced by "sexually active/sexually passive." The differences between these two categories of males are determined by the levels of their movement activity in the form of spontaneous flights. Various levels of moderate sexual activity, intermediate between these two extreme states, are obviously possible as well. It is males in this state which may attempt forced copulations (see below).

Transition from the passive state to that of active display by regular flights was observed by us in male no. 45, which from the moment of marking (1.VII) was constantly present in the part of the experimental plot embracing areas 2 and 3 (Fig. 2). During the second half of the day on 2.VII, this male kept together with two other males and was constantly coming into conflict with them, performing joint fluttering flights (see above). On 3 and 4.VII observations were not performed; on 5.VII, male no. 45 owned area 5 and made two contacts with females. It is interesting that the first of these contacts could be regarded as a forced capture of the female, whereas the second one ended in successful copulation. This male also copulated successfully twice on 9.VII (at 17.32 and 18.14). One more female visited its area at 18.08 but did not allow the courting male to mount it. On the same day, at 17.00, a pretender to area 5 appeared. After capture of a female by male no. 45, this newcomer approached the copulating tandem and tried to snatch the female out of it. By 18.00, the pretender became active in trying to occupy the main perch of male no. 45, after which

a typical process of owner replacement was observed. Male no. 45 was seen for the last time on 13.VII; it appeared for a short time in the place where it had been marked and then flew away at once.

It was established with certainty that a male forced out from its area could return after a few days of absence, regain its former area, and remain its owner for a sufficiently long time. For example, male no. 61 kept its area in a patch of aquatic vegetation from 16 to 19.VII. Within this period it was observed to mate 4 times. On the last day, its perch was occupied by male no. 70, which before this event had been observed for several days approximately 6–7 m to the left of the study plot. This change was preceded by a long conflict between the owner and the pretender. During the second half of the day on 19.VII, male no. 70 copulated 4 times (14.55–17.16); at about 6 p.m. male no. 61 started to reclaim the same area. On the following day male no. 61 quite easily forced male no. 70 out; the latter then moved to the right of the observation plot and later was not recorded there. As for male no. 61, he was recorded to have made an unsuccessful copulation attempt on 20.VII at 17.25 and also faint attempts at approaching two females which landed within its area at 17.35. All the above indicated a decrease in the sexual activity of this male during the second period of ownership of the area. However, the male kept the area until 24.VII, when our observations ended.

These and many other observations suggest that it may be possible to speak not only of an individual area of a male, which remains in his sole possession for a comparatively short time (several days), but also of his homerange overlapping those of many other males. The marking results showed that the same male could be encountered at various times in points located up to 80 m apart; this was confirmed, in particular, by observation of male no. 45 (see also Table 1). The male keeps within such a homerange before the onset of the peak of his sexual activity, when he begins to own the convenient perch, and also after the end of the period of active reproduction.

Attempts at Forced Copulation

Our observations show that the concepts of "non-territorial males" and "sneakers" should not be equated. An urge to capture a female given a good opportunity is inherent in each mature male. We have described a case when a male captured a female which

Table 2. The size and reproductive success of *C. splendens* males conditionally classified as "territorial" ones

Males (with record numbers)	Length of abdomen, cm	Number of copulations
Most successful		
61	3.94	4
45	3.8	4
70	3.8	4
Mean	3.86 ± 0.07	
Not very successful and unsuccessful		
64	4.03	1
138	4.0	1
63	4.01	–
102	4.07	–
136	3.97	–
109	3.89	–
Mean	3.99 ± 0.06	

Note: The difference in the abdomen length between successful, not very successful, and unsuccessful males was significant by the Mann-Whitney criterion ($p = 0.037$).

had just surfaced within the male's territory after oviposition. This attempt was not preceded by courtship; copulation did not occur because the female did not bring her genital opening in contact with the male's copulative organs.

We have also observed formation of tandems in the early morning hours when males had not yet occupied their areas and were mixed with females. At that time the dynamic density of individuals of both sexes which had spent the night there in groups was sufficiently high, facilitating random sexual contacts.

Successful copulation in calopterygid damselflies can be guaranteed only if the female "willingly" allows the male to grasp her on completion of the courtship (for details, see Panov et al., 2010). If the female is grasped by the male by force, she "refuses" to copulate and does not bring the tip of her abdomen to the male's copulative organ. During normal copulation, the male quickly flaps his wings several times after mounting, drawing the female up and thus helping her to take the proper position. When copulation is forced, such a series of flaps is sometimes repeated more than ten times (up to 13) but without any success[2].

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[2] See video in http://panov-ethology.ru/download/copula.mpg.

Forced captures of females were observed by us in banded demoiselle aggregations on the river Msterka where the dynamic density was exceptionally high. There, each capture of a female by a male attracted attention of many other males, so that in one case, a female was actively claimed by 4 males. All of them formed a dense tangle with the female submerged in the water (Panov et al., 2010, fig. 15).

According to the observations by Cordero and Andrés (2002) on demoiselles *Calopteryx haemorrhoidalis*, a typical attempt at forced copulation consists in the male grasping the female at the moment of oviposition. We have observed such behavior only once (out of 49 recorded copulations, of which 20 were observed from beginning to end). There were two successful and two unsuccessful attempts at snatching the female out of a tandem. Thus, such phenomena were quite rare in the damselfly aggregation studied by us; therefore we consider it unlikely that there exists a special category of males which "specialize" in snatching females.

DISCUSSION

The ideas discussed above seem to be in good agreement with the point of view, summarized in Koskimäki et al. (2009), that "studies on various *Calopteryx* spp. have repeatedly shown that territorial and non-territorial behaviors [of males] are conditional mating tactics and that body size does not predict [the male's] resource-holding potential and territorial behavior." The cited authors suggest that non-territorial males should be referred to as "wanderers" rather than "sneakers."

It has been shown that one of the factors affecting the male's reproductive potentials is the fat content in its tissues (Plaistow and Siva-Jothy, 1996). In particular, the reserves of this energy source are superfluous in young males which have not yet obtained individual areas, and gradually decrease with age, reaching the minimum by the moment the male leaves the area after keeping it for several days (up to 20 days in *C. maculata*: see Forsyth and Montgomerie, 1978). Our results seem to be quite compatible with this interpretation.

As for the problem of efficiency of attempts at forced copulation, such attempts seem to be characteristic of situations with very high dynamic density of males (as it was shown by observations on the river Msterka; see above). A similar situation was described

for very dense reproductive aggregations of *Calopteryx haemorrhoidalis*. In a plot with moderate density, 77% out of 96 copulations were preceded by normal courtship behavior of males, whereas in another plot, with high density, 60% out of 161 attempts at copulation were forced (Cordero and Andrés, 2002). It is difficult to suppose that all the forced captures of females were carried out by "sneaker" males. Strange as it may be, the cited authors did not reject the idea of "well-known" alternative reproductive tactics. Such is the force of belief in the truth of conventional assumptions.

According to the data on *Calopteryx haemorrhoidalis* (Cordero, 1999), 49 out of 53 cases of forced capture of a female (which in turn constituted 63.1% of 84 attempts) resulted in copulation. It should be noted, however, that according to the cited author, a male may use both modes of action: stimulating the female for copulation (which is traditionally ascribed only to "territorial" males) and forced mounts (which is believed to be "alternative sneaker tactics"). For example, the most successful male used the first mode 3 times and the second mode also 3 times, whereas 16 copulations could not be assigned to any of the two types (Cordero, 1999: 34). Since the duration of copulations of both types did not differ significantly, it can be admitted that forced copulations were also successful. We have also made some observations pointing to such a possibility.

Similar data were given in the work of Forsyth and Montgomerie (1987), who wrote that 14% of territorial males of *Calopteryx maculata* tried to snatch females within other males' areas. Such "trouble makers" were individuals which had emerged early in the season and had been "successful territorial males" before switching to this behavior.

The work of Koskimäki et al. (2009) may serve as an example of non-critical a priori subdivision of males into "territorial" and "non-territorial" ones (wanderers). They captured 39 males in the course of two days (18 and 28.VII). Of these, 28 males were classified into the category of "territorial" ones because they stayed for 3 hours within a 2-m radius and kept within 50 cm from the water surface. Those 11 males which did not meet these conditions were regarded as "wanderers." Having analyzed this small and formally composed sample, the cited authors concluded that territorial males were on average bigger than wanderers. In our opinion, conclusions based on the material collected in this way are not quite reliable.

We believe that the "classification" followed by the cited authors, as well as other similar classifications, cannot bring anything but ambiguity in the concepts of animal behavior. Such a priori schemes clearly contradict the principle of "Occam's razor" (entities should not be multiplied unnecessarily) and appear to be the basis of simplistic interpretations, taking the researcher away from detailed analysis of the phenomenon in all its complexity and inherent inconsistency.

REFERENCES

1. Contreras-Gurduño, J., Córdoba-Aguilar, A., Lanz-Mendoza, H., and Cordero, R.A., "Territorial Behavior and Immunity are Mediated by Juvenile Hormone: the Physiological Basis for Honest Signaling?" Functional Ecology **21** (1), 157–163 (2009).
2. Cordero, A., "Forced Copulations and Female Contact Guarding at a High Male Density in a Calopterygid Damselfly," J. Insect Behav. **12** (1), 27–37 (1999).
3. Cordero, A. and Andrés, J.A., "Male Coercion and Convenience Polyandry in a Calopterygid Damselfly," J. Insect Sci. **2** (14), 1–7 (2002).
4. Forsyth, A. and Montgomerie, R.D., "Alternative Reproductive Tactics in the Territorial Damselfly *Calopteryx maculata*: Sneaking by Older Males," Behav. Ecol. Sociobiol. **21** (2), 73–81 (1987).
5. Gould, S.J. and Lewontin, R.C., "The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme," Proc. R. Soc. Lond. B **205**, 581–598 (1979).
6. Grether, G.F., "Survival Cost of an Intrasexually Selected Ornament in a Damselfly," Proc. Biol. Sci., No. 264 (1379), 207–210 (1997).
7. Koskimäki, J., Rantala, M.J., and Suhonen, J., "Wandering Males are Smaller Than Territorial Males in the Damselfly *Calopteryx virgo* (L.) (Zygoptera: Calopterygidae)," Odonatologica **38** (2), 159–165 (2009).
8. Pajunen, V.I., "Aggressive Behavior and Territoriality in a Population of *Calopteryx virgo* L. (Odonata: Calopterygidae)," Annals Zool. Fenn. **3**, 201–214 (1966).
9. Panov, E.N., *Animal Behavior and the Ethological Structure of Populations* (URSS, Moscow, [1983] 2009) [in Russian].
10. Panov, E.N., Opaev, A.S., and Pavlova, E.Yu., "The Social Organization of Reproductive Aggregations and Mating Behavior in Calopterygid Damselflies (Insecta: Odonata)," Etologiya Zoopsikhologiya, No. 2, 1–31 (2010), http://www.etholpsy.ru/.
11. Panov, E.N. and Pavlova, E.Yu., "The Life of Dragonflies through the Eyes of an Ornithologist," Priroda, No. 11, 28–37 (2009).
12. Plaistow, S. and Siva-Jothy, M.T., "Energetic Constraints and Male Mate-Securing Tactics in the Damselfly *Calopteryx splendens xanthostoma* (Charpentier)," Proc. R. Soc. Lond. B **263**, 1233–1238 (1996).
13. Shorter, J.R., *Coloration as an Indicator of Male Quality in the Dark Winged Damselfly Calopteryx maculata* (2007), http://deepblue.lib.umich.edu/bitstream/2027.42/57583/1/.
14. Siva-Jothy, M.T., "Male Wing Pigmentation May Affect Reproductive Success via Female Choice in a Calopterygid Damselfly (Zygoptera)," Behaviour **136** (10/11), 1365–1377 (1999).