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MOBILITY OF THE RHEOBIONT DAMSELFLY *CALOPTERYX SPLENDENS* (HARRIS) IN FRAGMENTED HABITATS (ZYGOPTERA: CALOPTERYGIDAE)

G. SCHUTTE, M. REICH and H. PLACHTER
University of Marburg, Faculty of Biology, Department for Nature Conservation, Karl-v.-Frisch-Straße, D-35032 Marburg, Germany

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C. splendens is common along slow-flowing streams and rivers in central Europe. This sp. is well-suited for studies on the population structure and mobility of semi-aquatic rheobiont organisms. In this study the authors investigated a local population over a 2 km stretch of river in central Germany, by habitat analysis and mark-recapture-experiments. Emergent aquatic vegetation only influences density if the coverage is lower than 10%. Adult damselflies mainly use vegetation along the banks. Unused, moderately eutrophicated stands of herbaceous vegetation without trees and shrubs are preferred. Insolation in the morning is the primary factor for the selection of males' territories and thus determines the pattern of density. The investigated population turns out to be much bigger than expected. 2649 individuals have been marked individually (1543 ♂, 1106 ♀). 47% of the ♂♂ and 29% of the ♀♀ have been recaptured at least once. Most individuals migrated less than 300 m, which is roughly the home range size, but 23 individuals covered more than 1000 m. Three bridges spanned the investigated stretch of river. None of them caused a complete fragmentation of the habitat, but in the case of a wide but low bridge, more than 70% of the approaching damselflies turned back. However, 13% of all recaptured individuals successfully crossed at least one bridge.

INTRODUCTION

Because of the natural arrangement of habitats, local subpopulations of many species are partially isolated from one another. Partial isolation and local extinction are an important part of the survival strategy of species which are strictly dependent on patchy habitats. This is described by the metapopulation concept (GILPIN, 1987; GILPIN & HANSKI, 1991; LEVINS, 1970; REICH & GRIMM, 1996; SHAFFER, 1985). However, man's increasing habitat fragmentation and isolation through impacts and intensive land-use may lead to a reduction in abundance and a loss of species in continuous habitats. In this way, man-made habitat fragmentation proves to be an outstanding factor in the extinction of species in many modern landscapes (FAHRIG & MERRIAM, 1985; PLACHTER, 1996; SOULÉ, 1986; SAUNDERS et al., 1991). Strategies have been developed to reduce the level of fragmentation, i.e. by corridors or "habitat stepping stones" (HOBBS, 1992; JEDICKE, 1990; MADER, 1990; SAUNDERS & HOBBS, 1991).The effects of fragmentation have been studied for several terrestrial animals such as forest birds, small mammals, or ground beetles (OPDAM, 1991; MADER, 1979), but our knowledge of limnic and semi-terrestrial species is poor. Streams and rivers are often continuous even if they are heavily impacted, and habitat fragmentation therefore seems to play a minor role. However, even rather, "smooth" impacts like dense spruce afforestations on the banks can cause habitat fragmentation in semi--terrestrial insects (HERING et al., 1993).

Many dragonfly and damselfly species are rheobiont and strictly bound to running waters at the larval and adult stages. One of these species is *Calopteryx splendens*. It had been very common on many streams and rivers in central Europe, but the population has declined considerably during recent decades. *C. splendens* is therefore included on the German Red Data List as being "endangered" (CLAUSNITZER et al. 1984). It is well suited for studies on population structure and habitat fragmentation as the adults are usually confined to banks, where they often occur in large numbers, fly quite slowly, are distinguishable from other dragonfly species even over long distances and can be marked individually (cf. HEYMER, 1973; ZAHNER, 1960). We carried out a study on this species, stressing number and spatial distribution of adults within a local population and the influence of bridges spanning the river.

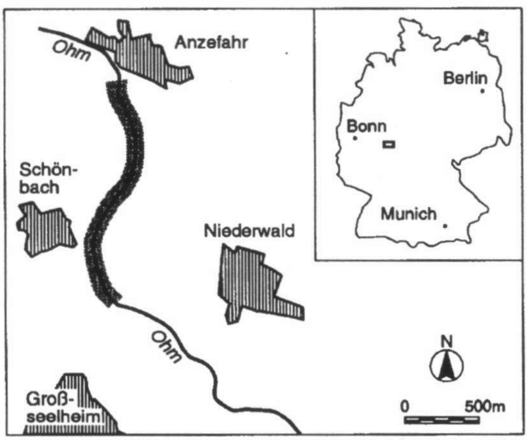
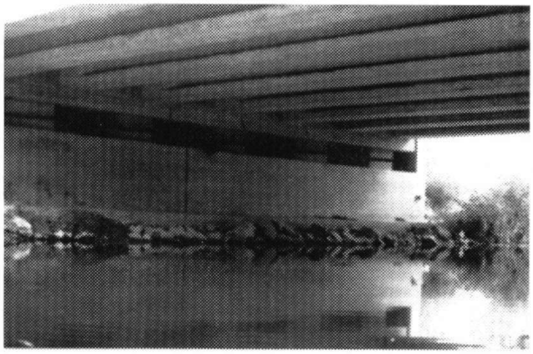


Fig.1. Location of the investigated stretch of the Ohm river; – inset: location in central Germany.

SITES AND METHODS

The field study was carried out between March and September 1993. A two kilometre stretch of the river Ohm was selected for the investigation. The Ohm is a small river (average width 20 m), situated in central Germany (State of Hesse), southeast of Marburg (Fig. 1). The banks and parts of the riverbed have been artificially altered producing a continuous incline of 0.04 % and a velocity of 0.1 to 0.3 ms^{-1} (max. 0.7 ms^{-1}).



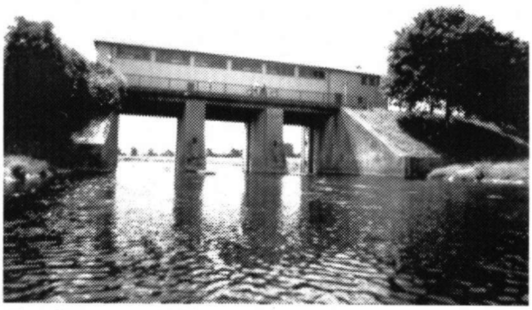


Fig. 2. Construction of bridge I (top) and bridge III (bottom).

Three bridges cross the river course along the selected stretch. Bridge I is 16 m wide and 25 m long (Fig. 2 top). The gap between the water level and the underside of the bridge was 2.0 to 2.3 m. During the period of investigation, light intensities on sunny days lay between 500 lux at the borders and 140 lux in the centre beyond the bridge (for comparison: light intensity in the shadow of a tree was about 11,000 lux). There is no vegetation on the riverbanks under the bridge. Bridge II is 9 m wide and 25 m long. The gap between water level and the underside of the bridge ranges between 2.9 and 3.2 m, the light intensity beyond the bridge is about 1,200 lux. One riverbank is continuously lined by a narrow stretch of vegetation. Bridge III is used to regulate the river (Fig. 2 bottom). The 3 openings can be closed by weirs during spring floods. Each opening is 6 m wide and 10 m long and crosses the river at a height of 5.5 m above water level. Light intensity beyond the bridge was recorded at 6,000 lux. Downstream, for a distance of 50 m, the river banks are paved and only very sparse vegetation is present there.

Both river banks are lined by more or less continuous stretches of vegetation, thus separating the banks from the adjacent agricultural land. As these stretches are the preferred habitat of adult *C. splendens* their plant species and societies were mapped. The quantitative vegetation analysis was carried out according to BRAUN-BLANQUET (1964). Both banks of the river were subdivided into segments of 25 m each and the borders were marked. There, the structure of the banks and the terrestrial and adjacent aquatic vegetation was recorded according to given structural types and phytocoenoses. The coverage of the aquatic vegetation was estimated in four classes (<10, 10-25, 25-40 and >40 %). Within the bank segments, the location of each *C. splendens* was determined to within +/- 5 m. Habitat preferences are indicated by the number of all records for the period of investigation per area.

Adults of *C. splendens* were observed and captured on 64 days between 16th of May and 30th of August 1993. They were captured with a net on being observed for the first time and individually marked with consecutive numbers on the lower parts of both hind wings, using quickly drying lacquer ("edding 780" and "edding 142"). Therefore specimens could be identified even if one of the wings got damaged after the first capture. Recording of "recaptures" was carried out by reading the number on the wing with the aid of binoculars. This avoided the need for further recaptures by net. *C. splendens* turned out to be a good model organism for mark--recapture-experiments. Apart from the qualities already mentioned, this species usually flies only small distances until it rests again and can therefore easily be recorded. It is extraordinarily resilient towards disturbances and does not even take flight after having been caught.

The reactions of adults on approaching the three bridges were recorded immediately over periods of eight hours each. The "fragmentation quality" for each bridge is expressed by the share of observed individuals not crossing beyond it. Mark-recapture data gave additional information on the number of individuals passing the bridges.

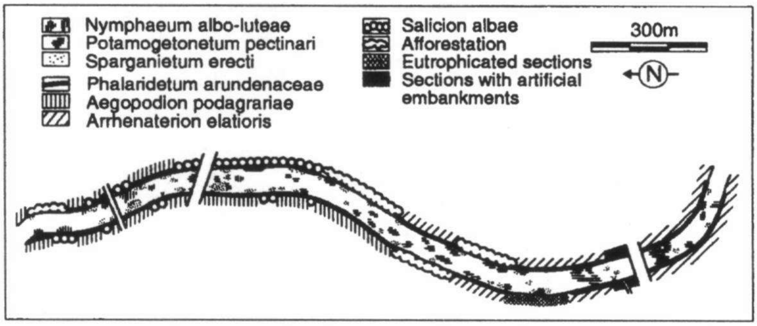


Fig. 3. Phytocoenoses along the banks of the investigated river stretch.

RESULTS

VEGETATION STRUCTURE AND HABITAT PREFERENCES

The density and composition of the aquatic vegetation varies widely along the river course. *Potamogeton pectinatus, Nuphar lutea* and *Sparganium erectum* are the dominant plants. Only 40% of the banks are covered by trees and shrubs (Fig. 3). Two structural types are present: 10 to 15 m high woodland edges consisting of *Salix fragilis* and *Alnus glutinosa* and recently planted woodlands with *Alnus*

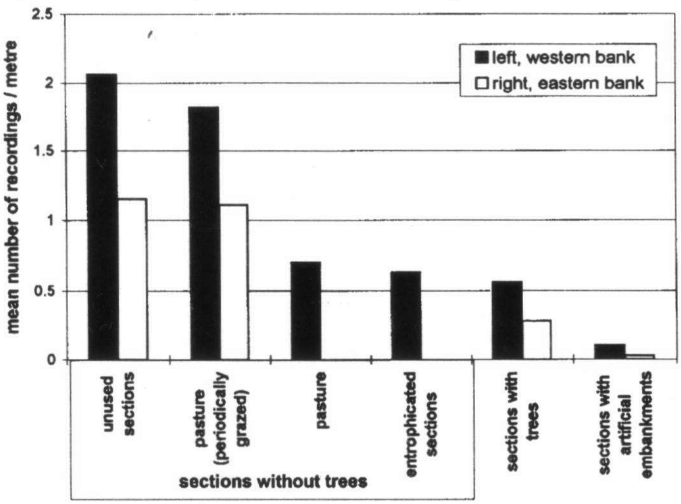


Fig. 4. Densities of adult *C. splendens* in different structural types of the banks along the river.

glutinosa, Salix sp., *Euonymus europaea* and *Cornus sanguinea*, 2 to 3 m in height. There, the herbaceous layer is dominated by *Urtica dioica*. The rest of the banks (60%) are covered with herbaceous vegetation only. The unused edges between the river and the agricultural land varies in width but rarely exceeds two metres. The dominant plant species are *Phalaris arundinacea, Urtica dioica* and - often in pure stands - *Bromus inermis*. If abandoned land borders the banks *Ceratophyllum bulbosum* and *Convolvulus sepium* are abundant. The agricultural land is mainly used as meadows (*Arrhenaterion elatioris*).

In total 4507 observations of *C. splendens* were analyzed with respect to the habitat structure. The left, western bank of the river Ohm is preferred by *C. splendens* regardless of habitat structure. More than 68% of all observations (3238) originate from this bank. Within the investigated river stretch, the density of *C. splendens* is clearly uneven. The highest density (3.23 observations per metre) is recorded in edges along the banks without trees and shrubs, while the lowest density (0.02 observations) occurred in a paved stretch of the right, eastern bank (Fig. 4). Within treeless edges, the density of observations is highest in unused, moderately eutrophicated herbaceous vegetation, while densities on heavily eutrophicated stands (*Urtica dioica*) are significantly lower. Cattle pastures return intermediate densities. These results are independent of age and sex of *C. splendens*. Woodland rims are constantly used, but the densities are rather low. The difference between old groups of trees (0.36 observations per metre) and recently planted trees and shrubs (0.34 observations) is not significant. The density above the water level is low, if the coverage of aquatic vegetation does not exceed 10 % (1.39 observations per metre). In the other classes of coverage, densities vary widely (Tab. 1).

Table I

Densities of observation of adult *C. splendens* relating to 5 classes of coverage of the emerse vegetation on the river

Coverage class (%)	No. of records (n)	Min./max. density (observ./m)	Average Ø
<10	5	1.3/1.6	1.4
11-25	18	0.8/4.3	2.3
26-40	10	1.2/3.6	2.3
>40	4	1.7/4.0	2.9

3920 observations refer to individuals resting on plants. Most of the 395 observations on aquatic vegetation relate to *Potamogeton pectinatus* (55,4%), *Sparganium erectum* (29,9%) and *Nuphar lutea* (13,2%) but the frequency of observations is correlated with the frequency of these plant species. Therefore, none of them seems to be preferred. In the terrestrial vegetation, *Phalaris arundinacea, Urtica dioica* and *Bromus inermis* are obviously preferred for resting. More than 95% of the 3525 observations on terrestrial vegetation relate to these three plant species. Although the three plant species are common, this share clearly exceeds their abundance.

Table II
Numbers of marked and recaptured individuals and recapture rates. – [rh = recently hatched, – sub = subadult, – ad = adult, – S = sum per sex]

	Males				Females				*Total*
	rh	sub	ad	S	rh	sub	ad	S	
Marks	92	383	1068	1543	117	317	672	1106	*2649*
Recaptures	27	181	520	728	28	114	182	324	*1052*
Recapture rate (%)	29.3	47.3	48.5	47.2	23.9	36.0	27.1	29.3	*39.7*

RECAPTURES AND POPULATION SIZE

In total 2649 adult (1543 ♂, 1106 ♀) *C.splendens* were marked, and 2150 additional observations of marked individuals are available. The average period between the first and last observation of a specific mature specimen is 8.1 days (♂: 9.2, ♀: 5.7 days). There are several recordings between 21 and 25 days. The longest period of recording is 49 days for a male and 26 days for a female. According to continuous records of emerging individuals, a time span of 10 days for postmetabolic maturation was estimated. Thus this span must be added to minimum lifespan calculations.

39.7% (1052) of the marked specimens (728 ♂, 324 ♀) were recaptured at least once. Proportions of recapture were lowest for recently hatched specimens (29.3/23.9%) (Tab. II). Most of the individuals were recaptured only once or twice, but single males were captured up to 14 times, whereas females were captured 6 times at the most. The average number of recaptures was 1.94 (2.1 ♂, 1.4 ♀).

To carry out mark and recapture experiments successfully, the size of the subpopulation should be appropriate, the share of marked individuals should exceed 20 % and the share of emigrating individuals should be low (MÜHLENBERG, 1993). A 2 km stretch of river seemed to meet these conditions. However, in the course of investigation, the local population turned out to be much bigger than expected. A fairly good recapture rate of 39.7% was obtained nevertheless. However, for a considerable time span in the middle of the investigation period, the share of recaptures was below 10%. Therefore, strictly speaking, population estimates like the Lincoln or Jolly indices are not applicable and indeed the results of the calculations differ in rates of magnitude. But the total brood of the local population doubtlessly exceeds 2650 damselflies. The application of the Jolly index, which is less sensitive to low recapture rates, results in a maximum population size of about 2000 specimens between 4th and 15th June.

MOBILITY

Mobility is indicated by the maximum distance between all observations of a

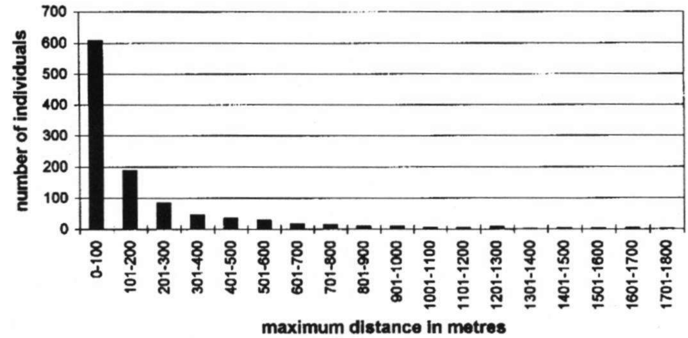


Fig. 5. Variance of the covered distance for all recaptured *C. splendens.*

specific individual along the river stretch. According to this, most of the marked specimens (606 individuals, 57.6%) covered a distance of less than 100 m (Fig. 5). 269 (25.6%) of the recaptured individuals moved over a distance of 100 m to 300 m and 154 (14.6%) over a distance between 301m and 1000 m. Only 23 specimens (2.2%; 20 ♂, 3 ♀) exceeded a distance of 1000 m, but one male flew as far as 1725 m. As can be proved by the results of individuals observed for more than 10 days, the recorded flight distance depends on the time span of observation. The median of specimens observed for more than 10 days is 165 m, whereas it is only 80 m for all recaptures. Generally males are more mobile. The median for males is 90 m, for females it is only 45 m. The maximum distance recorded for a female is 1475 m. Within all marked specimens there are no significant differences between males and females. However among the individuals which moved more than 300 m, males are significantly more abundant ($p < 0.05$) than females. Males dominate even more among flight distances more than 900 m. Obviously, 17 of the 23 individuals exceeding 1000 m preferred a distinct movement direction. 11 specimens consequently flew upstream whereas 6 specimens flew downstream. In May, the percentage of distances over 300 m was lower than during the rest of the investigation period, but there is no clear tendency during the summer.

FRAGMENTATION BY BRIDGES

235 events of *C. splendens* approaching one of the three bridges were recorded. Four different types of reaction could be distinguished (Tab. III):

- 88 individuals (37.5%) crossed along the river beyond the bridge without any noticable reaction;
- 5 individuals (2.1%) flew over the bridge;
- More than half of all individuals (n = 138; 58.7%) turned around in front of the bridge

Table III

Reactions of *C. splendens* adults approaching the three bridges. – [Numbers of observations: CB = crossing beyond, – CA = crossing above, – T = turning around, – P = falling down to the water line]

Locality	CB	CA	T	P
Bridge I	22	0	52	4
Bridge II	52	1	66	-
Bridge III	14	4	20	-
Total	*88*	*5*	*138*	*4*

and flew away in another direction;
- 4 individuals (1,7%) plunged down to the water before having crossed under the bridge. This reaction was only observed at bridge I.

None of the three bridges caused anything like total fragmentation of the population, but the effects differed significantly. Whereas at bridges II and III 51.9 and 52.6% respectively of the individuals turned back, it was 71.8% at bridge I. The sex ratio of individuals turning around in front of the obstacle was male biassed (65.4 % males at bridge I, 97% at bridge II and 80% at bridge III).

136 marked and recaptured specimens (102 ♂, 34 ♀), that is 13% of all recaptured individuals, successfully crossed at least one bridge. 23 of them (17 ♂, 6 ♀) crossed two, and 2 males even managed to cross all three bridges. Several specific adults crossed bridge I or II twice (15 ♂, 4 ♀) and some crossed bridge II as many as three times (3 ♂, 1 ♀).

DISCUSSION

Maximum lifespans for dragonflies in the field were recorded for several species, e.g. *Aeshna juncea* (85 days), *A. subarctica* (72 days) and *Lestes sponsa* (69 days) (CORBET, 1956; SCHMIDT, 1964). A male *Calopteryx virgo* survived for an estimated 51 days (HEYMER, 1973 according to original data from KLÖTZLI, 1971). In this study we observed one male of C. splendens for 49 days. Adding the maturation time, which is around 10 days, this male presumably survived for more than 59 days.

C. splendens is known to use a broad variety of habitats along running waters (REHFELDT, 1986). This is, in principle, confirmed in this investigation. However, *C. splendens* significantly preferred specific stands, especially those without trees and shrubs, and the western river bank. Within uncovered herbaceous banks, the density is highest in stretches not regularly used and is lower in heavily eutrophicated stands. Some plant species, being common in moderately eutrophicated stands are preferred as microhabitats for resting. The impact of adjacent agricultural utilization does not seem to reduce the habitat quality of the banks too severely. However, cattle pastures, which extend to the water level, lower the density of *C. splendens* significantly.

Males select their territory every morning. Sunny stands are preferred and are kept even if they become shaded later in the day (cf. HEYMER, 1973). Males, having acquired a sunny microhabitat, stay there during the day and defend it, while other males continue their search. Additionally, the structure of the emergent aquatic vegetation might be important for the males' choice of territories (REHFELDT, 1982) to offer the females an optimal habitat for egg deposition. Our investigation shows, that the percentage of coverage of the emergent vegetation does influence the density of dragonflies, but only, if it is lower than 10%.

BUCHWALD (1986) pointed out the coherence of insolation and aquatic vegetation. Completely shadowed stretches of streams and rivers are free of aquatic vegetation. The sum of insolation during the year not only depends on the number and density of the bank-lining trees and shrubs but also on their orientation. In the investigated stretch the course of the river Ohm is almost exactly north-south orientated. In the morning, when the males' territories are fixed, only the western bank is exposed to the sun. This explains the differences in density of adults between the banks. Thus, insolation of the habitat is obviously the primary factor for habitat selection. Secondarily, density is modified by the structure of the terrestrial and aquatic vegetation.

Cautiously estimated, the maximum population size of *C. splendens* was 2000 or higher. This means an average density of about 100 adults per 100 m, which is higher than recorded densities. REHFELDT (1986) recorded a density of 50 individuals per 100 m and BÖTTCHER (1986) declared 70 individuals per 100 m to be an overestimate.

Most of the marked individuals migrated less than three hundred metres. As males pursued regularly passing females over a distance of 120 to 150 m (cf. the much smaller distances given by ST. QUENTIN, 1964), this distance might indicate the home range of a male and can not be interpreted as dispersal activity. Only 16.8% of all recaptured dragonflies, but 29.4% of the individuals observed for more than ten days, covered a distance of more than 300 m. After all, 23 individuals covered a distance more than 1 km. Thus, the population on the investigated 2 km stretch should be regarded as a fraction of a continuous population along the Ohm river. Adults of *C. splendens* were occasionally recorded far away from an adequate stream habitat (cf. SCHUMANN, 1961). In our investigation, too, some specimens covered considerable distances, whereas most *C. splendens* adults remained more or less strictly in one place. Density stress is often recorded to be the trigger for emigration and long distance migration (for dragonflies MOORE, 1952; STETTMER, 1995). But in our investigation, this cannot be the reason, at least not the sole one because the share of flights exceeding 300 m was relatively constant over the whole investigation period and independent from the actual density. The share of flights exceeding 300 m is much higher in adult males than in females. This is striking, as most of the males keep strict territories. As the published data refer to males only (KLÖTZLI, 1971; PAJUNEN, 1966; ZAHNER, 1960) it is not clear, whether this is a general phenomenon in this species. But dispersal is obviously not restricted to recently hatched or subadult individuals as it is repeatedly stated in literature (CORBET, 1980; ROBERT, 1959).

None of the three bridges caused a strict fragmentation of the local adult population. Nevertheless, the effects are significant, especially in the case of bridge I. Two parameters might be responsible for the observed effect of partial fragmentation: the reduction of light and the loss of natural vegetation. The fragmentation effect is highest at bridge I, which is the darkest building because of its width and its height of only 2 m and which lacks vegetation on both banks. Strikingly, the number of crossing *C. splendens* is lowest at bridge III, where light intensity is scarcely reduced. But there the banks are paved and nearly free of vegetation over about 50 m. It is known, that *C. splendens* orientates itself by land marks, especially in the structure and the vegetation of the banks (HEYMER, 1973) and that individuals normally fly only 20 to 30 m without rest (ZAHNER, 1960). Therefore, long dark buildings or tubes as well as paved banks free of vegetation should have significant effects on the mobility within the adult populations of *C. splendens*. However, drift of larvae probably regularly occurs downstream and at least single females cross the bridges upstream. Therefore, in our case there is probably no substantial impact of the bridges on the survival rate or the genetic constitution of the local population.

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