Spatial variation of life-history traits in the freshwater snail *Bulinus truncatus*, the intermediate host of human and cattle schistosomiasis, in relation to field application of niclosamide in northern and central Côte d'Ivoire

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Abstract

Background: Control of intermediate host snails using molluscicides for the control and/or elimination of schistosomiasis is strategy in the line with WHO recommendations. Niclosamide is the main chemical molluscicide recognized by WHO. However, the extent of the application of molluscicide outside the immediate killing of the snail such as the impact on the evolution of life-history traits; in relation to recolonization of treated sites is less or not known. This study aimed to characterize the spatial variation of life-history traits in *Bulinus truncatus* populations in north and central Côte d'Ivoire, in relation to niclosamide spraying in the field.

From 2016 to 2018, we conducted a trial to control the intermediate host snails for interrupting seasonal transmission urinary schistosomiasis in northern and central Côte d'Ivoire, using niclosamide. The molluscicide was sprayed three times per year in habitats harboring the freshwater snail *B. truncatus*. Snails were collected before niclosamide application and 2-3 months after the sites were treated, and also from some untreated sites. Families from six natural populations of snails were monitored for several life-history traits, including growth, fecundity and survival, under laboratory conditions, over one generation (G_1).

Results: Survival rate varied among populations with the highest rates observed in northern populations. No significant difference was detected between populations before and after treatment, for this trait. Numbers of eggs and eggs per capsule at first reproduction, fecundity and growth were significantly lower in treated than untreated groups. Similar finding was observed for populations of before and after treatment. Egg production also varied across populations with the highest values found in northern populations. Within treated group, a significant difference for survival rate was detected between northern and central populations. Almost all parameters of reproduction and growth varied significantly, except for the number of egg capsules.

Conclusions: Our study shows a spatial variation of life-history traits in *B. truncatus* snails. Lower values of these traits were observed in populations from recolonized sites after treatment with niclosamide. This trend was much more perceptible in populations from central Côte d'Ivoire. Investigations should be carried out over several generations of snails in order to clarify the impact of niclosamide on their life-history traits.

Background

Schistosomiasis is the most important snail-borne disease, endemic in the tropical countries, with more than 90% of cases occurring in the WHO African Region and the highest proportion in sub-Saharan African [1–3]. Despite increasing efforts to control this parasitic disease, it still remains a public health concern in endemic countries, affecting approximately 260 million people [3] and leads to serious economic losses [4].

Transmission occurs in freshwater bodies, used intensively by both humans and livestock, where intermediate host snails and their associated schistosomes are present [5, 6]. Hence, the distribution of genera and species of intermediate host snails compatible with the schistosome parasite influence the distribution of the disease. Schistosome transmission cannot occur without compatible snails [7].

The World Health Assembly (WHA) recommended local schistosomiasis elimination “where feasible” to member countries such as Côte d’Ivoire, through resolution WHA65.21 [8]. Control intermediate host snails using molluscicides for the control and/or elimination of schistosomiasis is strategy in the line with WHO recommendations [9]. Niclosamide (Bayluscide®) is the main molluscicide registered and recommended by WHO [10]. Of note, schistosomiasis control projects conducted in Morocco, in China and in Egypt showed that snail control using this molluscicide could be an efficient approach for reducing or interrupting the transmission of schistosomes [11–13]. Moreover, recent systematic reviews and meta-analysis on the impact of the application of chemical molluscicides [14, 15] demonstrate the importance of integrating snail control using niclosamide towards schistosomiasis elimination campaigns in endemic areas [7].

Host snail populations of different environments are known to vary in biological features at regional and local geographical scales [16–18]. Efficient control of these snail populations therefore requires deep knowledge of their life cycle [19]. For that purpose, it is necessary to assess the life-history traits of individuals [20, 21]. These traits include growth, survival and reproduction, with age at first reproduction being one of these organizer parameters [22].

In this context, freshwater gastropods of the Hygrophila group offer excellent biological model. The snail *Bulinus truncatus* is one of these gastropods. In Africa and the Middle East, this snail acts as intermediate host for both *Schistosoma haematobium* and *S. bovis*, the agents of human and cattle schistosomiasis, respectively [23, 24]. *B. truncatus* is a hermaphroditic selfing species, with selfing rates as high as 80% in some populations [25]. Life-history traits can vary within and among populations under the influence of genetic and environmental factors [26–28].

Previous studies reported that the niclosamide is highly active at all stages of the freshwater snail life cycle; killing them within a few hours at low concentrations [7, 10, 14, 15]. However, the extent of the application of molluscicide outside the immediate killing of the snail such as the impact on the evolution of their life-history traits is less or not known. Nonetheless, pesticides are known to impact several biological traits of organisms [29, 30]. For instance, it has shown that chlorpyrifos and profenophos reduce survival rate, growth rate and egg production, and cause severe damages in the hermaphroditic gland cells of *B. truncatus* snails [31]. Therefore, niclosamide may influence the evolution of biological traits. It is thus important to know how life-history traits vary in *B. truncatus* populations in relation to habitat treatment with the molluscicide. We monitored several traits in six natural populations of *B. truncatus*, over one generation, under laboratory conditions, using a family design, in order to characterize the spatial variation of life-history traits in *B. truncatus* populations, in relation to niclosamide application in the field.

This study is part of a Schistosomiasis Consortium for Operational Research and Evaluation (SCORE) large-scale project [32] that aims to interrupt seasonal transmission of *S. haematobium* in northern and central regions of Côte d'Ivoire by combining chemical snail control using niclosamide and preventive chemotherapy with praziquantel [33].

Results

Survival rate of the populations

There was a variation for survival rate among snail populations. Survival rates reached 100% within the first three weeks, and decreased until week 12 ranging from 91.1% in DAT population to 48.9% in LBT population. The survival rate was higher in northern populations compared to the central populations from week 13 to week 18 (Fig. 1a). However, no significant difference was observed between untreated and treated groups (Fisher's exact test, $p = 0.674$). Within each group, no significant variation was detected among populations for untreated group (Fisher's exact test, $p = 0.249$), whereas for treated group the survival rate significantly varied among populations (Fisher's exact test, $p < 0.001$). There was no significant difference for survival rate between LBT and LAT populations (Fisher's exact test, $p = 0.079$).

Reproduction And Growth Of The Populations

Most of the parameters (8 over 13) of reproduction and growth significantly varied when comparing treated and untreated groups (Student's t-test, $p < 0.05$) (Table 1). Similar variation was observed before and after treatment for populations of LAT and LBT (Wilcoxon rank test, $p < 0.05$) (Table 2). Tables 1 and 2 show that the numbers of eggs and eggs per capsule at first reproduction, the mean fecundity as well as the growth were significantly lower in the treated populations compared to the untreated ones.

Table 1

Comparison of reproduction and growth parameters between *Bulinus truncatus* group from untreated and treated sites

Traits	Untreated group (84)	Treated group (90)	t	p-value
Age 1rep	76.05 ± 14.97	75.26 ± 17.87	-0.318	0.751
Size 1rep	3.75 ± 0.30	3.51 ± 0.47	-4.147	< 0.001
Nec 1rep	2.59 ± 1.37	2.10 ± 1.26	-2.472	0.014
Ne 1rep	6.61 ± 3.93	4.59 ± 3.70	-3.480	< 0.001
Nepc 1rep	2.57 ± 0.87	2.14 ± 0.96	-3.139	0.002
Nec	0.37 ± 0.14	0.36 ± 0.17	-0.220	0.826
Ne	1.27 ± 0.55	0.93 ± 0.58	-3.908	< 0.001
Nepc	0.41 ± 0.14	0.28 ± 0.16	-5.923	< 0.001
Hatching rate	0.63 ± 0.18	0.58 ± 0.26	-1.456	0.147
Growth	3.21 ± 0.37	2.94 ± 0.41	-4.526	< 0.001
Initial size	1.46 ± 0.14	1.56 ± 0.18	4.325	< 0.001
Final size	4.65 ± 0.44	4.55 ± 0.47	-1.420	0.157
k	0.07 ± 0.04	0.07 ± 0.04	0.298	0.766
Abbreviations: Age 1rep, Age at first reproduction; Size 1rep, Size at first reproduction; Nec 1rep, Number of egg capsules at first reproduction; Ne 1rep, Number of eggs at first reproduction; Nepc 1rep, Number of eggs per capsule at first reproduction; Nec, Number of egg capsules; Ne, Number of eggs; Nepc, Number of eggs per capsule; k, growth rate. Untreated group represents populations collected in test sites; Treated group represents populations recolonizing sites after niclosamide application. The number of G1 individuals analyzed by group are in parentheses. Age is in day; Size is in mm and represented by the snail shell height. Number of eggs per day or mean number of eggs is given as mean ratios of the number of eggs laid over lifespan. Growth estimates are given as mean ratios of the final height over initial height. k calculated on the basis of the von Bertalanffy model. $P < 0.05$ indicates that the difference is significant.				

Variation of the reproduction and the growth parameters between populations and within each population group is given in supplementary file (Additional file 1: Table S1). There was a significant variation for all reproduction and growth parameters among populations (One-way ANOVA, $p < 0.05$). Within treated group, variation was detected for several parameters, except for the number of egg capsules (One-way ANOVA, $p = 0.901$).

Table 2

Comparison of reproduction and growth parameters between *Bulinus truncatus* population found before and after treatment

Traits	LBT (19)	LAT (17)	w	<i>p</i> -value
Age 1rep	96.95 ± 13.11	99.47 ± 13.07	179.5	0.579
Size 1rep	3.86 ± 0.32	3.85 ± 0.35	160.5	0.987
Nec 1rep	1.63 ± 0.76	2.00 ± 1.32	178	0.581
Ne 1rep	4.74 ± 2.47	2.94 ± 2.36	93	0.028
Nepc 1rep	2.99 ± 0.94	1.46 ± 0.82	31.5	< 0.001
Nec	0.25 ± 0.09	0.21 ± 0.13	130.5	0.333
Ne	0.87 ± 0.41	0.41 ± 0.41	68.5	0.003
Nepc	0.38 ± 0.16	0.16 ± 0.12	46	< 0.001
Hatching rate	0.66 ± 0.19	0.33 ± 0.34	78.5	0.009
Growth	3.18 ± 0.33	2.88 ± 0.52	91.5	0.027
Initial size	1.45 ± 0.10	1.47 ± 0.15	201	0.195
Final size	4.59 ± 0.46	4.17 ± 0.35	82.5	0.012
k	0.03 ± 0.03	0.06 ± 0.05	238.5	0.015
Abbreviations: Age 1rep, Age at first reproduction; Size 1rep, Size at first reproduction; Nec 1rep, Number of egg capsules at first reproduction; Ne 1rep, Number of eggs at first reproduction; Nepc 1rep, Number of eggs per capsule at first reproduction; Nec, Number of egg capsules; Ne, Number of eggs; Nepc, Number of eggs per capsule; k, growth rate. LBT is Linguèbo population collected before niclosamide application; LAT is Linguèbo population collected after niclosamide application. The number of G1 individuals analyzed by population are in parentheses. Age is in day; Size is in mm and represented by the snail shell height. Number of eggs per day or mean number of eggs is given as mean ratios of the number of eggs laid over lifespan. Growth estimates are given as mean ratios of the final height over initial height. k calculated on the basis of the von Bertalanffy model. <i>P</i> < 0.05 indicates that the difference is significant.				

Few trait variations were observed within untreated group, which essentially concerned first reproduction parameters, mean numbers of egg capsules and eggs and growth rate. Variation in the age at first reproduction was higher within the treated group than within the untreated one. The average values varied from 64.98 days in DAT population to 99.47 days in LAT population for the treated group. In the untreated group, values ranged from 68.51 days in NWT population to 96.95 days in LBT population. However, most populations in the North such as DAT and NWT laid eggs earlier than those of the Centre namely LAT and LBT. The dynamic of egg-laying also varied across the populations (Fig. 1b). An increase of egg production up to a peak at 42th days was observed in some populations as NWT, SAT, KWT and LAT. The first peaks were observed in LBT and DAT populations at 28th and 35th days, respectively. At

the end of 70 days, the number of eggs laid were higher in northern populations than in central populations; the highest value being found in NWT population and the lowest in LAT population.

Correlations between reproduction and growth parameters in each population are reported in supplementary file (Additional file 1: Table S2). A negative correlation was detected between age at first reproduction and fecundity parameters in populations from untreated and treated sites, except for the LAT population. However, growth was positively correlated with number of eggs per capsule in the central populations. Principal component analysis (PCA) based on the most potential reproduction and growth traits of the six populations showed that the first two components accounted for 70.12% of the total variation observed in the PCA (Additional file 1: Fig. S1). Age at first reproduction was negatively correlated with fecundity and growth. The cluster analysis revealed three groups. The group I included individuals characterized by a slow growth, a low fecundity (numbers of egg capsules, eggs and eggs per capsule) and a late reproduction. The group II consisted of individuals with earlier reproduction, smaller size and larger number of egg capsules. This group was composed of individuals from Djemitedouo only. The third group (group III) was characterized as follows: a larger size at first reproduction, an important number of eggs and eggs per capsule. This group included individuals from Noumousso, Sambakaha and Kongobo.

Discussion

To our knowledge, this is the first study assessing niclosamide impact on the evolution of life-history traits in *B. truncatus* populations following field treatments.

Our findings show that at a temperature of 22 to 25°C, survival rate was 100% within the first three weeks, before decreasing among populations from 91% in DAT population to 49% in LBT population at week 12 and to 18% in LAT population at week 18. Such disparities among population survival rates have been observed in previous studies investigating resistance of *Bulinus* sp. at low and high temperatures [34–36]. More recently, 100% survival rates have been reported in *B. truncatus* snails from Cameroon maintained at temperatures of 16°C and 24°C for periods up to 25 weeks [37]. In another studies, about 88%, 50% and 20% of the *B. globosus* snails survived after 12 weeks at 15.5°C, 21.2°C and 25.8°C, respectively [38]. Together with our study, these results indicate that *Bulinus* sp. is susceptible to environmental or seasonal temperature fluctuations, and therefore to anthropogenic changes that may occur in their habitats. *B. truncatus* populations of the northern displayed a higher survival rate than those of the central from week 13 to week 18. This difference between areas might be explained by frequent fluctuations in snail size within and between habitats resulting from a variability in environmental and genetic factors [16, 23, 34]. Indeed, these factors including temperature, sunlight, bottlenecks and founding events, more important in the North than in the Centre, might have made northern snails more robust and provide them with a longer survival time to the chemical treatments. Survival rate was significantly higher in northern population than in central population within treated group, whereas no difference was observed for those of the untreated group. These observations might indicate that treatments are more effective on central populations which have low survival rates.

However, no difference between population of before (LBT) and after (LAT) treatment was detected at first generation, for this trait.

Variability in most of reproduction and growth parameters was observed between untreated and treated groups. Variation in several parameters was also detected between pre- and post-treatment populations. Interestingly, fecundity at first reproduction, fecundity, growth of both treated group and LAT population were significantly lower than those of the untreated group and LBT population. The difference between these traits could be due to the niclosamide treatment, as a result of an elimination of most fertile and larger snails replaced by least fertile and smallest individuals. This might be considered as a good outcome of the mollusciciding, as larger host snails are known to produce more eggs per capsule and more cercariae (when infected) [39–41]. In addition, a high variability of reproduction and growth parameters was found within treated group compared to untreated one. These traits could be adaptive ones, allowing snails to recolonize treated sites [42]. One should pay more attention to these life-history traits. Most populations from the North laid eggs earlier than those from the Centre. Moreover, the dynamic of egg-laying varied across the populations, with numbers of eggs laid higher in northern populations than in central populations. These observations might indicate that egg production of northern snails recolonizing treated sites was less influenced by niclosamide application.

Negative correlations were found between age at first reproduction with mean numbers of egg capsules, egg and eggs per capsules. Hence, snails which reproduced earlier, laid more egg capsules, eggs and eggs per capsule. This might be considered as an advantageous feature in the recolonization process of habitats following treatments. We can infer that the niclosamide applications had no perceptible effect on age at reproduction, as no significant difference was detected for this trait between populations before and after niclosamide application.

On the other hand, principal component and cluster analyses revealed an influence of the most varying traits among *B. truncatus* populations. Reproduction and growth parameters characterizing groups I and III could be due to population mixing as a result of snail migration [43–46]. Indeed, snail populations of these groups share the same watershed, that of the watershed of Bandama river.

Conclusions

Niclosamide application impact on *B. truncatus* snails appears satisfactory, on the whole. No major effect on survival, reproduction and growth was detected in snails recolonizing treated habitats. However, our study revealed an ability of snails to recolonize treated sites, and this was much more pronounced in central populations. Further investigations should be conducted over several snail generations for accurate assessment of niclosamide impact on life-history traits.

Methods

Study area

This study was carried out in the North (Bounkani and Tchologo regions) and in the Centre (Gbêkê region) of Côte d'Ivoire (Fig. 2). These areas are known to harbour *B. truncatus* [47–49] which is predominantly involved in the transmission of *S. haematobium*, *S. bovis* and the *S. haematobium* x *S. bovis* hybrid [50]. In those regions, the snail is mainly observed in man-made dam, which are subject to a marked seasonality characterized by a long dry season and a short rainy season [47]. In the northern areas, one control village namely Noumousso (10°06'25.67''N latitude, 05°08'30.81''W longitude) and two test villages Djémitédouo (09°17'05.87''N, 02°58'08.81''W) and Sambakaha (09°24'10.72''N, 05°06'21.24''W) were randomly chosen. In the central part, Kongobo (07°45'50.33''N, 05°28'33.99''W) and Linguèbo (07°30'16.36''N, 05°42'22.60''W) were selected as control and test villages, respectively.

Snail Sampling

In each study village, human-water contact sites were identified and georeferenced using a hand-held global positioning system (GPS; Garmin Sery GPS MAP 62, Olathe, KS, USA) device [33]. Snail surveys were carried out at each human-water contact in March 2017, June 2017, November 2017, March 2018 and June 2018. Before each snail sampling, physico-chemical parameters of the water were measured *in situ* using a pocket multi-parameter tester (HANNA® Instruments HI 98129 Combo, Woonsocket, RI, USA). The parameters measured were temperature, pH, conductivity and total dissolved solids (TDS). Snails were collected by the same two experienced collectors, using a long-handled scoop and/or forceps for a period of 15 min [51, 52]. Shortly after each sampling, snails were morphologically identified on the basis of standard identification keys to the species level [23, 53] and enumerated. Then, an appropriate volume of niclosamide solution (at concentration of 10 g/l) was applied along the bank of the test sites if *B. truncatus* was found (Fig. 3a).

The populations studied were composed of individuals from recolonized sites 2 to 3 months after treatment of Djémitédouo (DAT), Sambakaha (SAT) and Linguèbo (LAT); from untreated sites with niclosamide of Noumousso (NWT) and Kongobo (KWT); and individuals collected before treatment in Linguèbo site (LBT). The *B. truncatus* populations collected (G_0 generation) were transferred to the laboratory, placed between two layers of moistened cotton in a labelled petri dish [54] (Fig. 3b).

Experimental Design

According to the experimental protocol of the current study (Fig. 4), snails were reared following of a *common garden* approach, where individuals from different sites were raised together in the same controlled (laboratory) conditions [55]. Thus, the rearing room and water (30 mL of mineral water) were maintained at a temperature of 22 to 25°C and under a photoperiod of 12 L/12 D. During the rearing, G_0 snails were fed *ad libitum* with granules for aquarium fish and juveniles with boiled lettuce. Water was changed and food given twice a week in rearing boxes.

In the laboratory, G_0 snails from the same site were put together in a 1.5 L transparent plastic box for acclimatization. The following day, 20 G_0 individuals of each population were randomly chosen. Each G_0 snail was isolated in a 40 mL transparent plastic box filled with 30 mL of mineral water for G_1 offspring

production. Two to three days later, egg-layings were observed synchronously in the boxes. After hatching, 7 to 10 days after the first egg-laying, the offsprings were maintained with the parents in rearing boxes for approximately two weeks. Then, two to three G_1 offsprings including two in 15 G_0 boxes and three in five boxes, aged 10 to 14 days were chosen at random in each box to reach a sample of 45 G_1 snails for each population. These G_1 individuals were isolated and reared in the same rearing conditions as their parents.

Assessment Of Life-history Traits

Life-history traits of G_1 individuals were monitored over 28 weeks, including survival, fecundity, growth and hatching rate. Size (shell height and width) was measured once a week using a graph paper under binocular magnifying glass. This allowed the estimation of the size at first reproduction, as well as the growth. Individual survival was monitored three times a week by observation with the naked eye. Fecundity of each individual snail was evaluated while checking egg-layings twice a week: number of egg capsules, eggs and eggs per capsule. The age and fecundity at first reproduction were recorded. The numbers of egg capsules as well as eggs laid over 10 weeks were estimated using a binocular magnifying glass and recorded. Fecundity at first reproduction was defined as the number of egg capsules, eggs and eggs per capsule over seven days after the first egg-laying day. The hatching of eggs was also monitored every two days over two weeks. At the end of each week, the egg capsules laid in each box were collected using a plastic spatula and put in a petri dish containing mineral water. Egg capsules were checked every two days over two weeks and the number of hatched individuals was recorded in order to calculate the hatching rate per week of each population.

Statistical analysis

A normality test was first performed to assess the distribution and variance homogeneity of each quantitative parameter using the Kolmogorov-Smirnov test. Then, the parametric Student t-test was used to compare the reproduction and growth parameters between population groups from untreated sites with niclosamide (untreated group) and recolonized sites following the treatment (treated group). These same parameters were compared using the non-parametric Wilcoxon rank test between populations found before treatment (LBT) and after treatment (LAT) in Linguèbo. Survival rates were compared using the Fisher's exact test. Variation of traits between populations and within each group was tested using the parametric One-way ANOVA test. The non-parametric Spearman's rank correlation rho test was performed to assess the relationship between pairs of reproduction and growth parameters in each population. Snail groups were investigated using Principal Component Analysis (PCA). All statistical analyses were performed using the software R version 3.6.1.

Abbreviations

WHO: World Health Organization; WHA: World Health Assembly; SCORE: Schistosomiasis Consortium for Operational Research and Evaluation; MDA: Mass Drug Administration; PCA: Principal Component

Analysis; GPS: Global Positioning System; pH: Potential Hydrogen; TDS: Total Dissolved Solids; DAT, SAT and LAT: Djémitédouo, Sambakaha and Linguèbo populations collected 2 to 3 months after niclosamide treatment, respectively; NWT and KWT: Noumousso and Kongobo populations collected in untreated sites with niclosamide, respectively; LBT: Linguèbo population collected before niclosamide application; p = p -value; SD: Standard deviation; P_{pop} : Population p -value; P_{tgr} : Treated group p -value; P_{ugr} : Untreated group p -value.

Declarations

Ethics approval and consent to participate

This study was part of a large project entitled “Interrupting seasonal transmission of *Schistosoma haematobium* and control of soil-transmitted helminths in northern and central Côte d’Ivoire”. Ethical approval was obtained from the ethics committees in Switzerland: “Ethikkommission Nordwest- und Zentralschweiz” (EKNZ; reference no. UBE- 15/34; date of approval 15 April 2015) and Côte d’Ivoire: Comité National d’Éthique et de la Recherche, Ministère de la Santé et de Lutte contre le SIDA (reference no. 007/MSLS/CNER-kp; date of approval 2 February 2016) and Direction Générale des Productions et de la Sécurité Alimentaire, Ministère de l’Agriculture (reference no. 0163/MINAGRI/DGPSA/DPVCQ; date of approval 27 January 2015). The purpose of the study and procedures for field sample collection were explained to village authorities and their verbal agreement was obtained before conducting field surveys.

Consent for publication

Not applicable.

Availability of data and materials

The data used and / or analyzed during this study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors’ contributions

CKK, YNTTB and EKN conceived and designed the study. YNTTB and EKN supervised the study. CKK, YNTTB, NRD, MO, DS, AK and AKK followed up field surveys and collected field data. CKK collected laboratory data. YNTTB and SCG contributed to collecting laboratory data. CKK and YNTTB analyzed and interpreted the data. CKK wrote the first draft. YNTTB, JTC, RKA, NRD, MAE and EKN revised the manuscript. All authors read and approved the final manuscript at submission.

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Figures

Figure 1

G1 individuals from six natural populations of *Bulinus truncatus*. a Survival trends. b Egg laying dynamics. DAT = Djémitédouo population collected 2 to 3 months after treatment, SAT = Sambakaha population collected 2 to 3 months after treatment, LAT = Linguebo population collected 2 to 3 months after treatment, LBT = Linguebo population collected before treatment, NWT = Noumousso population collected in control site and KWT = Kongobo population collected in control site.

Figure 2

G1 individuals from six natural populations of *Bulinus truncatus*. a Survival trends. b Egg laying dynamics. DAT = Djémitédouo population collected 2 to 3 months after treatment, SAT = Sambakaha population collected 2 to 3 months after treatment, LAT = Linguébo population collected 2 to 3 months after treatment, LBT = Linguébo population collected before treatment, NWT = Noumousso population collected in control site and KWT = Kongobo population collected in control site.

Figure 3

a Niclosamide applying against *Bulinus truncatus* in Sambakaha, northern of Côte d'Ivoire. b Snails alive arranged in a petri dish according to Sellin and Roux (1974).

Figure 4

Schematic diagram of the experimental protocol for the study of the life-history traits.

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