When less is more: accounting for overcompensation in mosquito SIT projects

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Trends in Parasitology

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Spotlight

When less is more: accounting for overcompensation in mosquito SIT projects

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Compensation and overcompensation under field conditions are confirmed in *Aedes* mosquitoes recently by Evans *et al*.: equal or increased densities of emerging adults may thus result from reduced larval densities. Here the consequences when applying the sterile insect technique and provide recommendations to avoid counter-productive effects are discussed.

Tsetse flies are extraordinary creatures [1], at the pinnacle of viviparity, with the female laying one mature larva every 10 days that has been nourished in the uterus and may outweigh its mother. Yet, overcompensation in this insect, that is, obtaining more adults with fewer larvae is not possible. In contrast, container-dwelling *Aedes* mosquitoes are subjected to the ecological constraint of a larval microhabitat – often less than 200 ml – where numerous larvae must feed on a limited resource. This creates the perfect environment for compensation or overcompensation, where extrinsic mortality imposed at an early larval stage may result in a better survival of the remaining larvae, leading to an equal or increased density of emerging adults.

This is well explained in a recent article by Evans *et al.* [2], in which the authors present three scenarios and the respective consequences of mortality of young larvae through external suppression activities, on the density of the adults, that is, reduction in the case of an additive relationship,

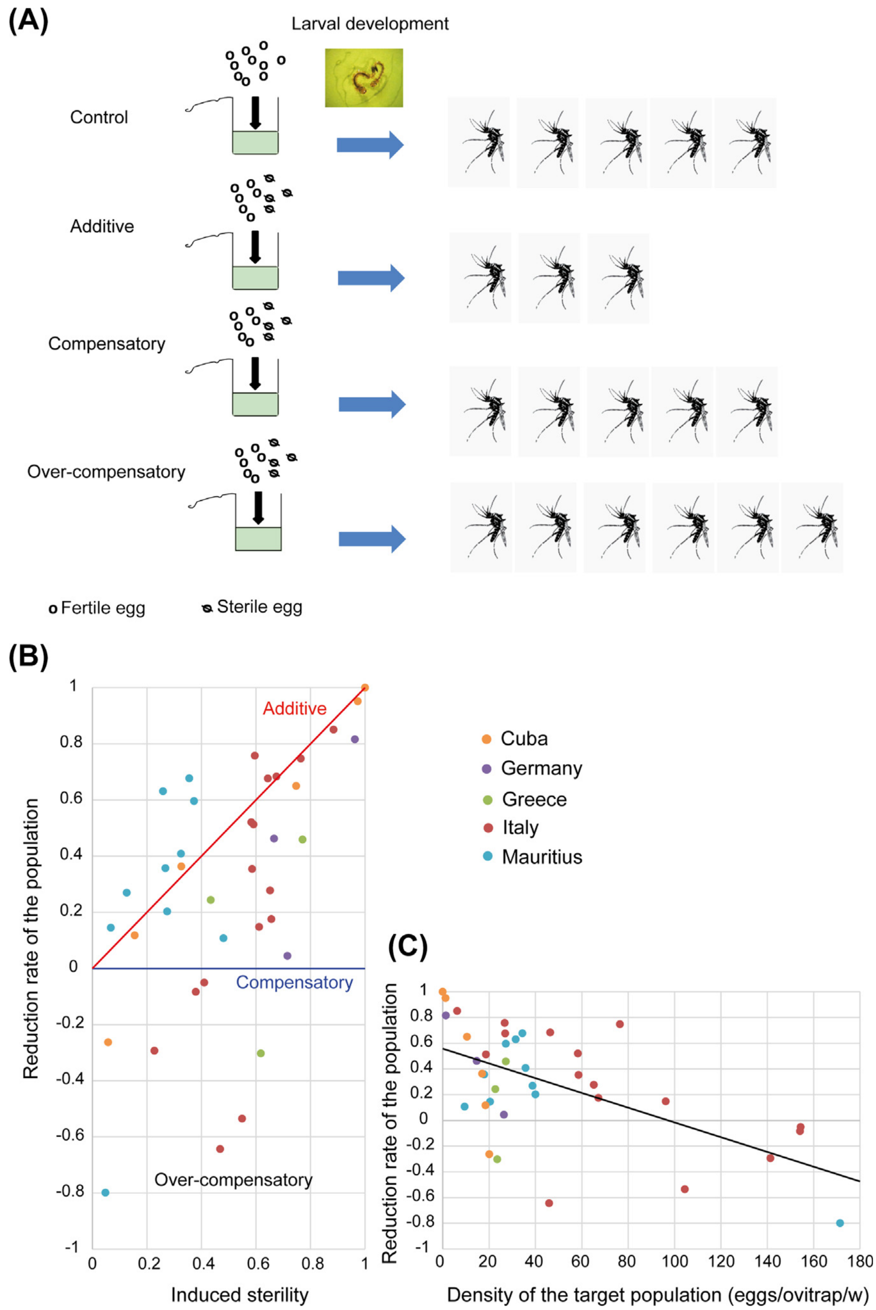

Figure 1. Impact of induced sterility on the density of the population in sterile insect technique (SIT) programmes. (A) Impact of imposing extrinsic mortality on eggs through the SIT depending on the relationship between initial larval density and the number of survivors. In the control group, the larval mortality is 50%. In the treatment groups corresponding to a 40% induced sterility, three situations are possible: a 70% mortality in the case of an additive relationship, superior to the control group; a 50% mortality in the case of a compensatory relationship, equal to the control group; and a 40% mortality in the case of an overcompensatory relationship, inferior to the control group. (B) Observed relationship between reduced egg density and induced sterility in five SIT trials. The reduction rate in egg density is calculated as a mean monthly average of row data (see

(Figure legend continued at the bottom of the next page.)

none in the case of compensation, and increase in the case of overcompensation (illustrated in Figure 1A). The authors demonstrated compensation or overcompensation in three *Aedes* species, in five out of eight experiments at five field sites. In one of them, they observed an almost fourfold increase in adults as a result of a ~50% decrease in larval density. In three experiments, the authors observed an additive relationship between initial larval density and the number of survivors.

The sterile insect technique (SIT) is a control tactic that is based on inundative releases of irradiated sterile males that induce female sterility, leading to embryonic death [3]: it is thus equivalent to early larval mortality. SIT is currently being applied against *Aedes* mosquitoes in pilot trials in 42 countries [4]. In SIT projects, 50% induced sterility (IS) in the target population, that is, half of the eggs hatching, is sometimes observed when the overflooding ratio is insufficient.

Raw data from five published SIT trials against *Aedes aegypti* and *Aedes albopictus*, aggregated by month (Figure 1B) was analysed. The reduction in egg density per trap per week in the release and untreated area, used as a proxy of the reduction in population abundance [5], was plotted against IS, a proxy of early larval mortality, to investigate which of the three scenarios presented above were observed. We found compensation or overcompensation in all the five datasets, with overcompensation being detected in at least one time point in four out of five. Furthermore, we observed that overcompensation was more likely at initial high egg densities, with a strong negative correlation between egg reduction rate and initial egg density in the release area (Figure 1C, Pearson's product-moment correlation of 0.56, $P < 10^{-3}$), confirming previous predictions [2].

In Cuba, where egg densities were relatively low (11 eggs per trap per week, S.D. 5), most time points showed an additive relationship, with the exception of the first month of release, when IS was low, leading to overcompensation (see Table S1 in the supplemental information online and additional references within). A similar situation was observed in Germany (egg density 14, S.D. 9), where only the first time point indicated compensation when IS was low. In Greece (egg density 24, S.D. 2), two data points showed an additive relationship and one compensation. In Mauritius, most time points also showed an additive relationship when egg densities were low (28, S.D. 9) but a strong overcompensation (79% increase of the densities) was observed during the last month of the trial, when a cyclone resulted in a population explosion leading to a more than six-fold increase in egg density. Finally, the most interesting situation was observed in Italy, where the egg density was overall high (72, S.D. 37): additive relationship for all time points with an IS of 0.7 or more, variable relationship from additive to compensatory for an IS of 0.6, and always compensatory or overcompensatory for IS <0.6, which also corresponded to high egg densities (100) (Figure 1C).

Furthermore, Evans *et al.* propose some 'general principles for enhanced effectiveness of control: (1) Imposing the maximum possible extrinsic mortality; (2) Targeting populations when larval abundances are low, (3) Knowing the shape of the survival-density response of the target species at the time and place control will be implemented'. Looking at the SIT projects presented above, these suggestions are fully supported and the following recommendations are provided for the specific case of mosquito SIT. For point (1), we recommend targeting an induced sterility >0.7 for which we observed only an additive relation. This will require an accurate estimation of the target population size [4], an appropriate production capacity to enable the release of the required numbers of sterile males to reach the necessary sterile-to-wild male ratio [5], a sterile male competitiveness above 0.2 [6], and targeting isolated areas or implementing buffer areas to prevent immigration of gravid fertile females from neighbouring areas. This last recommendation is another argument for applying SIT within an area-wide perspective, that is, addressing the entire vector population [7]. Regarding point (2), we observed compensation and overcompensation only for egg densities >20 per trap per week. In temperate areas, reduction of populations during winter may represent an ideal opportunity to apply SIT [8], although limited by the presence of overwintering eggs in the environment. Most of the time, the use of other suppression techniques prior to SIT releases, particularly source reduction, is recommended to reduce egg density to a level where the efficiency of SIT will be maximal thanks to its inverse-density-dependent properties. Once again, the SIT is not a standalone technique [7]. In Singapore, such a strategy has demonstrated its benefits over time [9]. Regarding point (3), this parameter will have to be included in Phase 1 (baseline data collection) of SIT programmes [4].

In conclusion, although the importance of compensation and overcompensation has clearly been underestimated, applying SIT against mosquitoes in an area-wide integrated pest management perspective [10] following a phase conditional approach may be the ideal strategy to deal with this impressive resilience property of *Aedes* mosquito populations.

additional references in Table S1), comparing the release and control areas. The relationship is additive when points are close to the red line, compensatory when they are close to the horizontal blue line, and overcompensatory when the reduced density is negative (increased egg density in the release area). (C) Observed relationship between reduced egg density and egg density in the release area in five SIT trials.

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Declaration of interests

The author declares no conflicts of interest.

Supplemental information

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References

1. Bouyer, J. (2020) *Glossina palpalis gambiensis* (Tsetse fly). *Trends Parasitol.* 36, 864–865
2. Evans, K.G. *et al.* (2023) Survival-larval density relationships in the field and their implications for control of container-dwelling *Aedes* mosquitoes. *Insects* 14, 17
3. Dyck, V.A. *et al.* (2021) *Sterile Insect Technique: Principles and Practice in Area-wide Integrated Pest Management*, CRC press
4. Bouyer, J. *et al.* (2020) Phased conditional approach for mosquito management using the sterile insect technique. *Trends Parasitol.* 36, 325–336
5. Carrieri, M. *et al.* (2011) *Aedes albopictus* (Diptera: Culicidae) population size survey in the 2007 Chikungunya outbreak area in Italy. I. Characterization of breeding sites and evaluation of sampling methodologies. *J. Med. Entomol.* 48, 1214–1225
6. Bouyer, J. and Vreysen, M.J.B. (2020) Yes, irradiated sterile male mosquitoes can be sexually competitive! *Trends Parasitol.* 36, 877–880
7. Vreysen, M.J.B. and Klassen, W. (2021) Area-wide integrated pest management and the sterile insect technique. *Sterile Insect Technique*. In *Principles and Practice in Area-Wide Integrated Pest Management* (2nd edn) (Dyck, A. *et al.*, eds), pp. 75–112, CRC Press
8. Douchet, L. *et al.* (2021) Comparing sterile male releases and other methods for integrated control of the tiger mosquito in temperate and tropical climates. *Sci. Rep.* 11, 1–14
9. Ng, L.C. (2021) *Wolbachia*-mediated sterility suppresses *Aedes aegypti* populations in the urban tropics. *medRxiv* Published online June 17, 2021. https://doi.org/10.1101/2021.06.16.21257922
10. Hendrichs, J. *et al.* (2021) *Area-wide Integrated Pest Management: Development and Field Application*, CRC Press