Human population growth and the extinction of the tsetse fly

Robin S. Reid a,*, Russell L. Kruska a, Uwe Deichmann b, Philip K. Thornton a, Stephen G.A. Leak a

a ILRI, P.O. Box 30709, Nairobi, Kenya
b United Nations Statistics Division, 2 United Nations Plaza, New York, NY 10017, USA

Received 15 February 1999; received in revised form 7 June 1999; accepted 19 July 1999

Abstract

Agricultural expansion is a major cause of biodiversity loss worldwide. In Africa, biologists have observed that the populations of some tsetse species, which transmit human and livestock trypanosomosis, decline or disappear as human populations grow and farmers clear fly habitat for cultivation. The objectives of this paper are to synthesize the available information concerning human and tsetse populations and to develop a model to estimate the future effect of human populations on tsetse populations. A spatial, GIS model was developed to estimate future impacts using a combination of fine-resolution human population data for the years 1960, 1980, 2000, 2020, and 2040; field data on the relationships between human and tsetse population densities; and the distribution of different types of tsetse fly. By 2040, many of the 23 species of tsetse fly will begin to disappear and the area of land infested and number of people in contact with flies will also decline. However, none of the species of flies will be under threat of extinction by human agricultural activities in the near term. An area of Africa larger than Europe will remain infested by tsetse and under threat of trypanosomosis for the foreseeable future. ©2000 Elsevier Science B.V. All rights reserved.

Keywords: Land-use; GIS; Trypanosomosis; Biodiversity; Africa

1. Introduction

Human modification of ecosystems is reducing biological diversity worldwide (Ehrlich, 1988; Wilson, 1992), most commonly caused by habitat loss during the expansion of agriculture (Wilcove et al., 1998). One possible case of human-driven extinction concerns the 23 species of tsetse fly (Glossina spp.) which are endemic to the African continent. Several species of tsetse are expected to decline in numbers as human populations grow, tsetse habitat is cleared and its wildlife hosts are reduced in numbers (Jordan, 1986). Thus, human population growth may eventually cause the extinction of the tsetse fly.

More is at stake than species extinction – this African fly can be considered a ‘critical structuring species’ (e.g., Holling et al., 1995) in human and ecological systems across 10 million km² of the continent. Tsetse flies transmit trypanosomosis, a parasitic infection that causes morbidity and mortality in several livestock species and in people. Wildlife species are the principal vertebrate hosts for trypanosomosis, but usually are unaffected by the disease, unless under stress (Jordan, 1986). However, over 29 million
people. 45 million cattle and unknown millions of sheep and goats in Africa are at risk of contracting trypanosomosis (or sleeping sickness in people) from the tsetse fly (calculations by the authors from data of Deichmann, 1996; Ford and Katondo, 1977; WHO/FAO, 1979). On the other hand, the tsetse fly is considered by some (Ormerod, 1978; 1986; 1990) to be the guardian of African ecosystems, preventing people and their livestock from over-using vast areas of the continent. Thus, if human population growth extirpates the tsetse fly in the near future, rural Africans may see short-term health benefits but longer term environmental costs. Environmental costs could include loss of wildlife populations and habitat (and thus income-earning opportunities), loss of ecological goods and services from wildlands (e.g., water recycling, soil erosion protection, natural genetic diversity, access to fuelwood and timber) and loss of soil fertility. Possible disappearance of the fly also suggests the need for a major redirection of current research in trypanosome and tsetse biology, host immunology, and the socio-economic and environmental impacts of tsetse control.

This paper reports the results of testing the old hypothesis that human population growth will cause the decline and extinction of the tsetse fly across Africa. The overall objectives of this paper is to synthesize the available information concerning human and tsetse populations and to develop a model to estimate the future impact of human populations on tsetse populations. This is now possible because the authors developed the first, fine-resolution GIS coverages of future human populations for the African continent for this analysis. These coverages were combined with in-depth field observations of the relationship between the densities of people and flies to create scenarios of tsetse and trypanosomosis across Africa in the mid-21st century.

2. Methods

2.1. Synthesis of information on human and tsetse populations

To develop future scenarios, all the available information about the relationship between human and tsetse populations was synthesised. Most of this information came directly from published accounts. In one case, the authors overlaid maps of human population density with maps of different fly species appearing in Jordan (1963) to obtain information about this relationship for Nigeria and Cameroon.

2.2. Tsetse scenario development

Once published data were synthesised, the first step in scenario development was to establish a quantitative relationship between human population density and tsetse populations from published accounts. Biologists who have attempted to quantify this relationship differentiate the effects of human population density on the three different groups of tsetse fly, distinguished by their preferred habitats: *morsitans* flies (five species) prefer open savanna woodlands, *palpalis* flies (five species) prefer riverine vegetation, and *fusca* flies (thirteen species) prefer forested habitats (Jordan, 1986). For example (see results for details), only savanna and forest flies are affected strongly by human use. Thus, future scenarios for fly populations were only developed for savanna and forest, but not riverine, flies. In addition, this synthesis (see below) showed that this relationship differed from place to place, so two scenarios (one conservative, one liberal) were developed that captured the range of variation in the relationship between human and tsetse population densities.

The second step was to develop fine-scale, GIS coverages showing estimated, future human populations for the African continent. Before this analysis, human population projections were available only at a national-level resolution (UN, 1997). Such a coarse resolution is inappropriate for this analysis because it does not match the resolution of the data on the distribution of tsetse species; tsetse data were collected during ground surveys of populations at a landscape scale (Ford and Katondo, 1977; Katondo, 1984). To estimate future human populations, fine-resolution GIS layers (1.4 million, 5 km × 5 km-grid cells) of population densities for 1960, 1970, 1980, and 1990 for the continent of Africa developed by U. Deichmann (Deichmann, 1996) were used. Human populations in the year 2000 were derived by calculating the grid-cell-by-grid-cell growth rates between 1980 and 1990. The rates for this rather than earlier decades...
were used because they best represent the reduced migration into unsettled rural areas expected in the future because of continued high rural-urban migration (Foote et al., 1993). For the years 2020 and 2040, it was found that the cell-based growth rates resulted in country-level human populations that were higher than the ‘medium’ UN country-level projections for the same years (UN, 1997) because the growth rates did not account for the expected decline in fertility and the effect of AIDS on African human populations. Therefore, after 2000, the projected aggregate population totals for each country were uniformly adjusted to match the UN population projections.

The final step was to use the quantitative relationship between the densities of people and flies (described above) to predict future tsetse populations. This was done by distinguishing three general classes describing the effect of human populations on fly populations: (1) a lower class where human populations are so low that they have no effect on tsetse populations, (2) a moderate class where human populations are associated with a decline in tsetse populations, and (3) a higher class where human populations are high enough to extinguish tsetse populations. Human population maps for the years 1960, 1990, 2020, and 2040 were then grouped into these three classes and then overlaid with the distribution of each fly group (Ford and Katondo, 1977; Katondo, 1984) to create scenarios of the changes in the health of tsetse populations between 1960 and 2040.

3. Results

3.1. Synthesis – relationships between human and tsetse populations

Not all three groups of tsetse flies (savanna, forest and riverine flies) are affected by human use. In particular, tsetse biologists have observed a decline in populations of savanna and forest flies as growing human populations clear fly habitat for cropping and reduce wildlife species on which these flies feed (Nash, 1948; Ford, 1971; Putt et al., 1980; Jordan, 1986; Rawlings et al., 1993; the author’s calculations from Jordan, 1963; Hendrickx, 1999). By contrast, some species of riverine flies can survive in densely populated villages by living among human-made structures or in groves of trees planted near dwellings (Baldry, 1970; Gouteux et al., 1982; Okoth, 1982; Jordan, 1986; Hendrickx, 1999).

For savanna flies, the most detailed observations were made by Nash (1948) concerning the species G. morsitans in Nigeria (Table 1). Nash compared the state of tsetse populations with existing human populations in different parts of Nigeria. He wrote (Nash, 1948; p. 9), ‘Generally speaking, G. morsitans occurs in areas with population densities ranging from 0 to 40 per square mile; occasional flies of this species are found in areas of 40–100, but never when the population exceeds 100, to the square mile’ (see Table 1 for conversion into km²). His work is supported by tsetse surveys in Lafia Division, Nigeria, in 1954–1956, where populations of G. m. submorsitans and G. longipalpis, two species of savanna fly, were already in decline when human populations were about 14 people km⁻² (Putt et al., 1980). In surveys in 1976–1978, when human populations had reached 61 km⁻² in Lafia, these species had disappeared from the entire division, save a protected forest area (Putt et al., 1980). In Togo, species of G. morsitans submorsitans, and G. longipalpis were rarely found in areas with more than 50 people km⁻² (Hendrickx and Napala, 1997; G. Hendrickx, unpublished data). Recently, Rawlings et al. (1993) both contradicted and supported these observations in The Gambia for G. morsitans submorsitans. In 12 of 19 rural districts (63%), tsetse populations still existed in areas with more than 40 people km⁻². In the remaining seven districts with greater than 40 people km⁻², no G. m. submorsitans was left. Jordan (1986) claims that the Gambian situation is relatively unique with the interspersion of bushy areas growing on lateritic soil in areas where human populations are high.

The evidence for a relationship between human population density and populations of the forest flies is similar to that of the savanna flies. In Togo, G. Hendrickx (unpublished data) shows that G. fusca is not found in areas with more than 50 people km⁻². In Nigeria and western Cameroon, forest flies declined strongly as human population density increased in different locations (Jordan, 1963). For spot records, 71% were found in areas with less than or equal to 38 people km⁻², 19% were found in areas with 39–77 people km⁻², and only 10% were found in areas with >77
Table 1
Synthesis of quantitative field data on the relationship between human and tsetse population densities (s: savanna fly, r: riverine fly, f: forest fly)

<table>
<thead>
<tr>
<th>Tsetse species (group)</th>
<th>Human population density at which tsetse decline</th>
<th>Human population density at which tsetse disappear</th>
<th>Location of study and citation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Glossina morsitans</em> (s)</td>
<td>15–39 people km(^{-2})</td>
<td>&lt;39 people km(^{-2})</td>
<td>Nigeria(^a)</td>
</tr>
<tr>
<td><em>G. m. submorsitans, G. longipalpis</em> (s)</td>
<td>14 people km(^{-2})</td>
<td>at least by 61 people km(^{-2})</td>
<td>Nigeria(^b)</td>
</tr>
<tr>
<td><em>G. m. submorsitans, G. longipalpis</em> (s)</td>
<td>unknown</td>
<td>at least by 50 people km(^{-2})</td>
<td>Togo(^c)</td>
</tr>
<tr>
<td><em>G.m. submorsitans, G. longipalpis</em> (s)</td>
<td>unknown</td>
<td>40% of districts, &lt; 40 people km(^{-2})</td>
<td>The Gambia(^d)</td>
</tr>
<tr>
<td><em>G. fusca</em> (f)</td>
<td>unknown</td>
<td>50 people km(^{-2})</td>
<td>Togo(^e)</td>
</tr>
<tr>
<td><em>G. fusca</em> (f)</td>
<td>unknown</td>
<td>rarely found in areas with &gt; 77 people km(^{-2})</td>
<td>Nigeria and Cameroon(^f)</td>
</tr>
<tr>
<td><em>G. medicorum</em> (f), <em>G. tabaniformis</em> (f)</td>
<td>unknown</td>
<td>&lt;77 people km(^{-2})</td>
<td>Nigeria and Cameroon(^g)</td>
</tr>
<tr>
<td><em>G. nighofusca</em> (f)</td>
<td>unknown</td>
<td>rarely found in areas with &gt; 77 people km(^{-2})</td>
<td>Togo(^h)</td>
</tr>
<tr>
<td><em>G. palpalis, G. tachinoides</em> (r)</td>
<td>low populations at 61 people km(^{-2})</td>
<td>unknown</td>
<td>Nigeria and Cameroon(^i)</td>
</tr>
<tr>
<td><em>G. palpalis</em> (r)</td>
<td>unaffected</td>
<td>unaffected</td>
<td>Togo(^j)</td>
</tr>
<tr>
<td><em>G. tachinoides</em> (r)</td>
<td>populations show gradual decrease as land becomes occupied by cultivation</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)Nash, 1948.  
\(^b\)Putt et al., 1980.  
\(^c\)Hendrickx, 1999; unpublished data.  
\(^d\)Rawlings et al., 1993.  
\(^e\)Jordan, 1963; Table 2.

...people km\(^{-2}\) (authors’ analysis). Of the six species, only one, *G. fusca*, was found in areas with more than 77 people km\(^{-2}\). In Uganda, populations of *G. fuscipes* (a forest fly) declined in areas where human populations had recently increased (Okoth, 1982).

By contrast, the riverine flies appear to be largely unaffected by human population density and can even adapt to human-made environments with a few important exceptions (Jordan, 1986). In Busoga, Uganda, although *G. pallidipes* (a savanna fly) and *G. brevipalpis* (a forest fly) declined as human populations increased, another species, *G. fuscipes* (a riverine fly), co-existed with people living in dense settlements (Okoth, 1982). In Lafia Division, Nigeria, *G. palpalis* and *G. tachinoides* (also riverine flies) still existed (although in low numbers) when human populations were 61 km\(^{-2}\) (Putt et al., 1980). Hendrickx (1999) showed that *G. palpalis* populations are unaffected by land-use in Togo. However, Hendrickx also showed that populations of *G. tachinoides* do decrease as land-use intensifies. Similarly, Bourn (1983) suggests that the removal of riparian forests (which is favoured habitat for riverine flies) will reduce the extent of riverine flies, especially at the drier limit of their range (where forest is restricted to wet areas).

The relationship between human population density and tsetse populations of savanna and forest flies is related directly to the amount of land under cultivation (and the hunting pressure on wild hosts). In an analysis of Zambia, Mali and Burkina Faso, human population density was related strongly to the amount of land cultivated (Reid and Ellis, 1995; Reid et al., 1995). Below 15 people km\(^{-2}\), an average of 12% of the land is cultivated in these three countries. Above 39 people km\(^{-2}\), more than two-thirds of the land is cultivated, and above 77 people km\(^{-2}\), over 95% of the land is cultivated. In semi-arid West Africa, the practice of fallowing disappears when human populations reach between 50–85 km\(^{-2}\) (Goddard et al., 1975). Synthesis of additional data from McIntyre and colleagues (McIntire et al., 1992; pp. 8 + 9) shows that fallowing disappears at about 85 people km\(^{-2}\) in 33 sites spread from the semi-arid to humid zones across Africa. Once the practice of fallowing ends, agricultural fields coalesce and remnant patches of tsetse habitat disappear.
Table 2
The two sets of classes used to create the liberal and conservative scenarios to estimate future tsetse populations

<table>
<thead>
<tr>
<th>Human population density (people km$^{-2}$)</th>
<th>State of tsetse populations</th>
<th>Average cropping intensity (%)$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Classes for the liberal scenario</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;15</td>
<td>high</td>
<td>&lt;12</td>
</tr>
<tr>
<td>15–39</td>
<td>declining</td>
<td>12–66</td>
</tr>
<tr>
<td>&gt;39</td>
<td>very low</td>
<td>&gt;66</td>
</tr>
<tr>
<td>Classes for the conservative scenario</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt;30</td>
<td>high</td>
<td>&lt;50</td>
</tr>
<tr>
<td>30–77</td>
<td>declining</td>
<td>50–95</td>
</tr>
<tr>
<td>&gt;77</td>
<td>very low</td>
<td>&gt;95</td>
</tr>
</tbody>
</table>

$^a$From a previous analysis of the relationship between human population densities and cropping-use intensity for Zambia, Mali and Burkina Faso (Reid and Ellis, 1995; Reid et al., 1995).

In summary, populations of savanna flies decline when human populations rise above 15 km$^{-2}$ and disappear altogether when they reach between 40 and 60 people km$^{-2}$. Many species of forest fly disappear when human densities rise to between 38 and 77 people km$^{-2}$. In some areas, riverine flies decline before human populations reach 60 km$^{-2}$, whereas in others, their populations are unaffected by human population density. These ranges were used to create two sets of classes (one liberal, one conservative) that bracket the quantitative data depicting the relationship between human and tsetse populations (Table 2). The next section describes the results of the application of these classes to develop future scenarios of populations of savanna and forest flies.

3.2. Future scenarios of fly populations

By the year 2040, the distribution of tsetse flies will contract in different areas across Africa, but will not disappear (Figs. 1, 2). About 50–60% of the 8 million km$^2$ currently infested with these flies will sustain high fly populations and an additional 15–20% of the area will support moderate fly populations. The greatest decline and contraction in savanna fly populations will occur in West Africa, the Lake Victoria Basin, northwestern Uganda, the coastal areas of East and southern Africa, and parts of central Africa (see black and dark gray, Fig. 1). Significant populations will remain in eastern, central, and southern Africa (see light gray, Fig. 1). Forest flies will disappear from most of coastal West Africa and large patches of the central African interior. The small patches of forest flies currently infesting eastern and southern Africa may disappear entirely by 2040. The liberal and conservative scenarios principally differ in the speed that tsetse populations decline over time rather than in the location of this decline.

The percentage of people within the original fly distributions who will remain in contact with high populations of savanna and forest flies will decrease substantially in the future (Fig. 3a). In 1960, about a third of rural Africans lived in scattered settlements where savanna and forest tsetse populations were high; this will fall to about 5% by 2040. Most people (95%) will live in areas free of savanna and forest flies.

Even though a smaller proportion of people will live in contact with savanna and forest flies in the future, the total number of people in these zones will not decrease greatly between 1960 and 2040 (Fig. 3b). In 1960, 10–20 million people lived in areas with these flies; by 2040, 5–17 million people will still live in these fly-infested areas. Consequently, millions of people and their livestock will still be at risk of contracting trypanosomosis.

4. Discussion

In African ecosystems, the tsetse fly strongly influences ecosystem processes because it is a vector of important human and livestock diseases (trypanosomoses). In the past, epidemics of sleeping sickness depopulated villages in Uganda and Tanzania (Ford, 1971); currently, in some areas, the presence of trypanosomosis can prevent the expansion of agriculture because farmers have little access to healthy draft oxen (e.g., in Ethiopia, Reid et al., 1999; Reid, 1999).
Fig. 1. Future scenarios of the effect of human population growth on savanna and forest flies, showing both liberal and conservative scenarios.

Fig. 2. Two scenarios of the amount of land area (ha) with high populations of savanna and forest flies between 1960 and 2040.
In other areas, the disease that the fly transmits only slows the spread of agriculture, rather than preventing its spread altogether (Erdelen et al., 1994). Thus, the decline and extinction of the tsetse fly is having from moderate to strong effects on the state of ecosystems across the continent.

The analysis in this paper shows that the tsetse fly will not become extinct in the next century; however,
there will be significant shifts in the type and distributions of flies present. Savanna and forest flies will be in decline all over Africa; some species in these groups may approach extinction. In contrast, riverine flies appear to be affected little or not at all by human population growth and are thus likely to remain extant indefinitely. Nearly 7 million km$^2$ will remain infested with riverine flies in 2040, an area significantly larger than Europe (assuming that the riverine fly distribution mapped by Ford and Katondo (1977) remains unchanged in the future). These areas are in western and central Africa; no riverine flies exist in eastern and southern Africa. It is, thus, only in eastern and southern Africa that human population growth may eradicate the fly from some areas altogether.

Despite the reduction of many tsetse fly species, human population growth will only cause a 7% contraction in the overall tsetse fly distribution by 2040 (solely in areas with no riverine flies). Veterinary programs currently control the fly over about 1% of the total area infested in eastern and southern Africa (Allsop, 1999). Barring breakthroughs in control, tsetse flies will be widespread in Africa for a considerable time.

How might the reduction of tsetse vectors affect the incidence of human trypanosomosis in the future? The severe form of sleeping sickness is transmitted by savanna flies (*Trypanosoma brucei rhodesiense*) whereas the chronic form (*T. b. gambiense*) is transmitted by riverine flies (Jordan, 1986). Thus, only the severe form, transmitted by savanna flies, will be affected by human population growth. This reduction will only occur in eastern and southern Africa where the severe form is found.

In contrast to human sleeping sickness, animal trypanosomosis is found throughout the 10 million km$^2$ of Africa infested with tsetse flies (Jahnke et al., 1988). A reduction of tsetse fly populations by human population growth should enhance livestock health if the distribution of livestock follows that of people. Evidence suggests that it does. The density of tropical livestock units (TLU’s) in five African countries was positively correlated with both the percentage of land cultivated and the human habitation density (Bourn and Wint, 1994). A GIS analysis by the authors showed a significant positive correlation ($r = 0.55$) between human and livestock population densities for the continent. The results shown here for people are thus probably also applicable to livestock.

That savanna flies are more affected by human population growth than forest or riverine flies has large significance. Of the three groups, these flies not only transmit the severe form of human sleeping sickness, but they have the highest trypanosome infection rates (Putt et al., 1980; infection rates of 20–25% for savanna flies, 3–25% for forest flies and 5% for riverine flies) and thus are the most efficient vectors of trypanosomosis. Moreover, these species can be difficult to trap (Jordan, 1986), and so the options for control are correspondingly limited. Human population growth will consequently have the greatest effect on the most efficient vectors of the disease and cause a greater proportional decrease in trypanosomosis risk than would be expected simply from a consideration of the area infested.

Despite the logic of the inverse relationship between human and tsetse populations, there will be exceptions to this pattern. Flies may be abundant in heavily populated areas because of the existence of small but crucial patches of tsetse habitat (Rawlings et al., 1993). *G. pallidipes*, a savanna fly, survived in low numbers in heavily cultivated areas among remnant trees in Tanzania (Swynnerton, 1936). Felling of forest and repeated burning by encroaching human populations can create ideal new habitats for savanna flies (Jordan, 1986). In Togo (Hendrickx, 1999), even though *G. tachinoides* populations declined as human populations grew, the prevalence of trypanosomosis in cattle remained a serious problem. As more and more land was cropped, cattle were pushed into marginal riverine habitats and thus came into increased contact with tsetse.

These scenarios suggest a different strategy for trypanosomosis control in the future. If the most efficient vectors of the disease are on the decline, most of the people and livestock in contact with the fly will be under low to moderate rather than high disease risk. In such cases, ‘partial’ disease control measures to treat affected people and animals, such as drugs and insecticidal dips, will be increasingly appropriate and effective. Larger-scale vector control strategies, which generally are more expensive or require more labour/cooperation, can then be reserved for use in communities still facing heavy tsetse infestations and those that have strong incentives for allocating public resources to tsetse control.
Over the shorter term, the predicted disappearance of tsetse fly populations from some areas will increase human and livestock welfare both directly, through better health, and indirectly, through better food production resulting from greater use of livestock. The longer term costs and benefits of regional disappearances of the fly are unknown. But reliable human population growth rates for Africa are now available to help predict where and when ecosystems will change, and thus scientists are better placed to determine the long-term costs and benefits of changes on the continent. This higher-quality research information is urgently needed by decision-makers, who face increasingly hard choices as human populations grow and the pressures on ecosystems escalate.

Acknowledgements

The authors thank B. Perry, J. Ellis, B. Swallow, J. Slingenburgh, and G. Hendrickx for stimulating discussions during the course of this work, O. Okello for excellent technical assistance, and J. McDermott and S. MacMillan for thoughtful reviews. The work was partially supported by grants from the Rockefeller Foundation and the International Fund for Agricultural Development (IFAD) to R.S.R and R.L.K.

References


Ormerod, W.E., 1978. The relationship between economic development and ecological degradation: how degradation has
occurred in West Africa and how its progress might be halted. J. Arid Environ. 1, 357–379.