
A die-off of large ungulates following a *Stomoxys* biting fly out-break in lowland forest, northern Republic of Congo

Paul W. Elkan^{1*}, Richard Parnell¹ and J. L. David Smith²

¹International Programs, Wildlife Conservation Society, 185th & Southern Blvd., Bronx, NY 10460, U.S.A. and ²Department of Fisheries and Wildlife, University of Minnesota, 1980 Folwell Ave., St. Paul, MN 55108, U.S.A.

Abstract

Understanding the role of natural die-offs or severe population declines is of significant importance to the management and conservation of large mammal populations. A die-off of bongo and other large ungulates occurred following a *Stomoxys* biting fly out-break in the lowland forest of the northern Republic of Congo in April–May 1997. Direct observations, remote camera surveys and monitoring within forest clearings indicated that the *Stomoxys* outbreak contributed to significant mortality in the bongo population and affected local distribution. Mortality was higher in adult males than in females. Male biased *Stomoxys* related mortality was also observed in sitatunga. Understanding of the causes and impact of such die-offs on bongo and other species are important to conservation and management planning in Central Africa.

Key words: mortality, Republic of Congo, *Stomoxys*, *Tragelaphus spekei*, *Tragelaphus eurycerus*

Résumé

Comprendre le rôle des hécatombes ou des graves diminutions naturelles des populations est d'une importance significative pour la gestion et la conservation des populations de grands mammifères. Il y eut une hécatombe de bongos et d'autres grands ongulés suite à une apparition massive de la mouche piqueuse *Stomoxys* dans la forêt de basse altitude du nord de la République du Congo en avril-mai 2007. Des observations directes, des études à distance par caméra et le contrôle continu dans les clairières forestières ont montré que la pullulation des *Stomox* contribuait à une mortalité significative dans la population des

bongos et affectait sa distribution locale. La mortalité était plus forte chez les mâles adultes que chez les femelles. Cette mortalité due au *Stomox*, biaisée vis-à-vis des mâles, fut aussi observée chez les sitatungas. Il est important de comprendre les causes et les impacts de telles hécatombes de bongos et d'autres espèces pour la planification de la conservation et de la gestion en Afrique centrale.

Introduction

Die-offs of large mammal populations because of drought, disease, starvation, habitat change, and predation have been documented throughout the world and in a variety of habitat types (Young, 1994, 1999; Erb & Boyce, 1999). The frequency and extent of these population declines need to be considered in conservation projections for large mammal populations. *Stomoxys* sp. flies (commonly known as 'stable flies') are widely known to cause stress and condition loss in large domestic and wild mammals. In extreme cases, they have caused death in large domestic mammals in Africa (Zumpft, 1973; Kunz & Monty, 1976; Radostits *et al.*, 2000). In wild populations, *Stomoxys*-associated mortality has been reported for bushbuck (*Tragelaphus scriptus*, Pallus) in the Aberdares, Kenya and lions (*Panthera leo*, Linnaeus) in Ngorongoro crater, Tanzania (Fosbrooke, 1963; Mihok & Clausen, 1996).

Bongo (*Tragelaphus eurycerus*, Ogilby), historically occurred in a discontinuous distribution along the lowland forest–savanna transition zone of Western and Central Africa and in isolated populations in East African montane forests (Ralls, 1978; Kingdon, 1982; Hillman, 1986). Western populations are declining throughout their range as a result of over-hunting and habitat loss, and rising exploitation by safari hunting and have been nearly extirpated in Kenya (East, 1999; Kingdon, 1997). Some of the highest abundances of bongo on record in Central

*Correspondence: E-mail: pelkan@wcs.org

Africa forests occur in the Tri-national area of Congo, Central African Republic and Cameroon (Elkan, 2003).

In this paper, we assess a die-off of bongo and other large ungulates that followed a *Stomoxys omega* outbreak in the Nouabale-Ndoki National Park and adjacent Kabo logging concession, northern Republic of Congo in April–May 1997. The general events surrounding the outbreak, associated mortality and relevant monitoring data collected in the years before and after suggest a locally important impact on the region's bongo population. This event of unusual high mortality has direct implications for conservation strategies, safari hunting regulation, and understanding factors influencing bongo distribution and abundance in Central Africa.

Methods

Study area

The Ndoki-Likouala region of northern Republic of Congo supports a semi-dry lowland type of primarily Sterculiaceae-Ulmaceae semi-deciduous forest, *Raphia* swamp forest, *Gilbertiodendron dewevrei*, and naturally occurring forest openings (Letouzey, 1968). Climate is equatorial with an annual precipitation of *c.* 1600 mm and an average annual temperature of *c.* 25°C. Four annual

seasons are generally described: long dry (December–February), short wet (April–May), short dry (June–July) and long wet (September–November).

Nouabalé-Ndoki National Park (NNNP) (Fig. 1) was established in 1993 to preserve one of the last remaining wilderness areas in Central Africa (Fay, Agnagna & Moutsambote, 1990). NNNP is contiguous with the Dzanga-Sangha National Park in CAR and Lobeke National Park in Cameroon. The NNNP is surrounded on the south, east, and north by forest management units (FMU) designated for commercial timber exploitation. A safari hunting operation exploited areas of the Kabo and Pokola concessions in 1995–1998 targeting trophy male bongo. The Government of Congo banned bongo trophy hunting in 1999.

Both the NNNP and FMUs contain forest clearing habitat (locally called 'bais' and 'yangas') important for large mammals. The Mombongo area of the Kabo FMU (Fig. 1), contains a network mosaic of small forest openings over a 6 km² low lying area used by forest elephant (*Loxodonta africana cyclotis*), bongo and other species. The Mbeli forest clearing (0.75 km²), in the NNNP, is used by western lowland gorilla (*Gorilla gorilla gorilla*, Savage and Wyman), sitatunga (*Tragelaphus spekei*, Sclater), elephant, and other species for feeding and drinking. A gorilla ecology and forest clearing investigation was started in 1993 at Mbeli and an

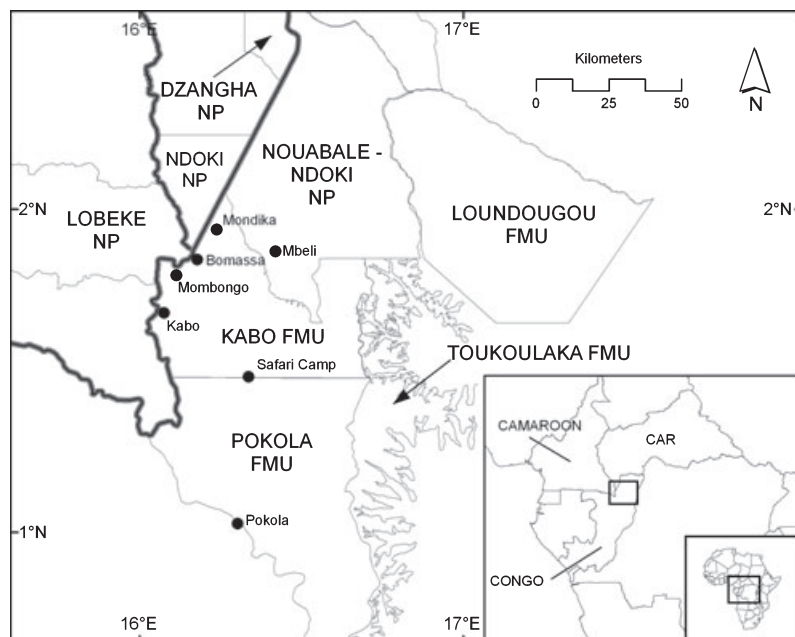


Fig 1 Nouabalé-Ndoki National Park and forest management units (FMU) in Republic of Congo and adjacent protected areas in Cameroon and Central African Republic

investigation of bongo populations and forest clearing ecology was begun in 1995 in Mombongo.

Specimen data

When it became apparent that a die-off was occurring, foot and vehicle surveys were undertaken along logging roads and in the forest to locate and document animal mortality. Carcass data collection included estimated time since mortality, age/sex, location and habitat type, estimated proximal cause of death and collected skulls and/or mandibles.

Direct observations

Observations from tree platforms at Mombongo and Mbeli generated information on large mammal visitations and the effects of the flies on animal behaviour. Observations were undertaken opportunistically in 1996–1997 in Mombongo in the evening, night, and early morning. Mbeli was systematically monitored with a semi-permanent daily presence during daylight hours (07.00–16.00 hours) 1995–2001. During fifteen consecutive days of bongo presence at Mbeli in May 1997, hourly scan observations recorded bongo location, condition and activity.

Bongo and other species were also observed while walking and driving in the Kabo FMU. Information was collected on species, age/sex category, behaviour, body condition and response to flies.

Camera trapping

Large mammal populations using the Mombongo area were monitored with remote cameras during 1996–2001. Eight Trailmaster remote camera units were randomly deployed among 35 clearings in a 6 km² area. Cameras were re-deployed at new locations in the forest-clearing complex every seven nights with an est. 35 trap nights × 8 units for an overall est. 280 nights/survey. This sampling was repeated in the wet, dry, and transition seasons of each year (September/October, January/February, May/June). Cameras were also deployed at three other areas of bongo activity in the Kabo concession at 6, 12 and 40–50 km from Mombongo to generate preliminary information on ranging.

Bongos were identified by stripe pattern, scars, horn shape and markings resulting in resighting histories for individual adult males and females. Photos of left and right

flanks were analysed separately. Photographic rates (number bongo photo/trap night) were assessed to compare estimated relative abundance before and after the outbreak (Carbone *et al.*, 2001).

Road surveys of large mammals activity

We surveyed large mammal sign along 16 km of logging road in the Mombongo area monthly. An observer assisted by two local trackers recorded observations of all sign (tracks, dung, etc.) following standard methods (White & Edwards, 2000). Sign encounter rate was analysed using paired comparisons taking into account seasonality. When animals walked continuously along the road only the first observation was used in analysis.

Results

Environmental factors

In mid-March 1997, a large nonbiting fly, identified as *Fainia elongata bezzi*, was observed to increase in the area. Although they did not bite, their swarming was an annoyance to both animals and humans. *Fainia elongata bezzi* remained in high abundance in May when they decreased rapidly. By late May, they were observed only in low numbers.

Small biting flies, *Stomoxys omega*, were first noticed in late March. These flies were observed in abundance through the end of May/early June (9–10 weeks) when they rapidly decreased (Fig. 2). *Stomoxys* bites were painful and caused a high level of discomfort to animals and humans. The flies swarmed animals in large numbers biting to extract blood.

General observations in subsequent years (1998–2001) suggested that both *Fainia elongata bezzi* and *Stomoxys* flies were noticeably present during the same period, that is, April–May each year. However, both species were in much lower numbers and present during a shorter period (2–3 weeks) than observed in 1997.

Rainfall patterns showed that a severe and long dry season in January–February 1997 was followed by heavy rains in March–May (Fig. 3). In 1997, dry season rainfall was very low (19 mm) compared to average rainfall (73 mm) for the same period in 1996 and 1998–2000. The short wet season in 1997, had high rainfall (419 mm) compared to the same period in other years (average 299 mm). Although the rainfall pattern in 2001 was

Fig 2 Frequency and time frame of bongo and yellow-backed (YB) duiker carcass encounter in relation to the *Stomoxys* outbreak in the NNNP and Kabo FMU in 1997

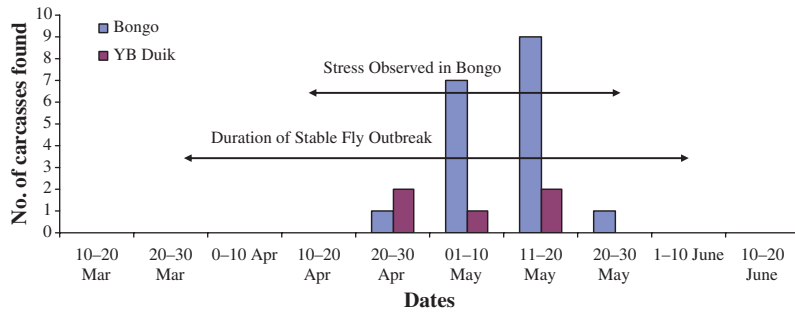
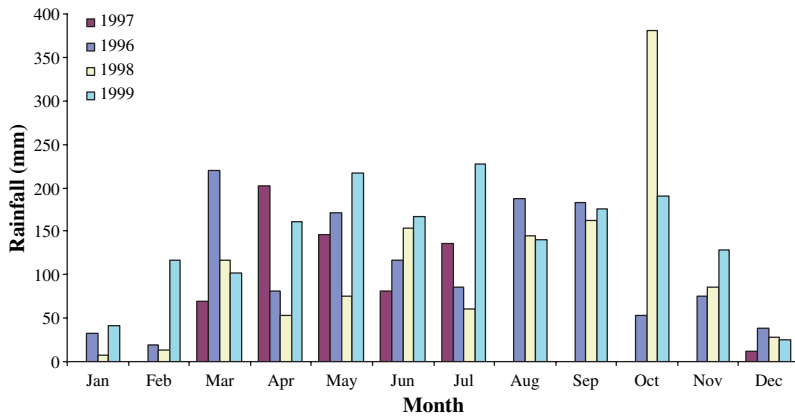


Fig 3 Rainfall patterns in the Ndoki region during 1996–1999



similar to that of 1997, no major fly outbreaks were observed.

Bongo behaviour

Observations of the effects of *Stomoxys* on the behaviour of bongo and other large mammals suggested a chronologically clear and distinct pattern (Table 1). Bongo behaviour before and after the *Stomoxys* outbreak was quite different from that observed during April–May 1997, when large numbers of biting *Stomoxys* surrounded and covered all bongos encountered. During this period, bongos were observed (n = 22 obs.) along logging roads and in forest openings during the hottest daytime hours (08.00–17.00 hours). They walked for exceptionally long distances along roads (sometimes >3 km) and frequently rested in the open, appearing tired, weak, and in poor condition. As fly numbers dropped in early June, bongo behaviour and habitat use patterns returned to previous normal patterns: bongo fleeing quickly upon sighting humans and visitation of clearings predominantly during the evening and night. No abnormal behaviour, as was observed during the

Stomoxys outbreak, was recorded in the years of study before or afterward.

Bongos were never observed at Mbeli during the first 3 years of the study. In mid-April, at the peak of the *Stomoxys* outbreak, four adult males visited the clearing for several hours. Subsequently two of the males continued to visit, both appearing to be in good condition. In 176 hourly scans over 15 consecutive days in May, the two males stood with their legs partly submerged in the stream in the same location during 86% of daylight hours. They shook and turned their heads during 84% of the time, simultaneously dipping ears into the water in an attempt to escape from insects.

In early May, the condition of one animal noticeably deteriorated; the ribs became more visible as weight dropped and pelage became dull. The second male also appeared to lose weight, but to a lesser degree. The carcass of the weaker male was found near the clearing at the end of May. No signs of predation were found. The second male visited the clearing regularly until late May and was again re-sighted in late June. No bongo sightings were registered at Mbeli during the following 4 years of monitoring until an adult male visited in April 2002 (E. Stokes, pers. comm.).

Table 1 Ungulate behaviour observed during March–June 1997 in relation to outbreak of *Stomoxys* flies

Date	Observation
Early and mid-March	No unusual behaviour noted in the Mombongo area: bongo used forest clearings at night and foraged along roads in the early morning and late evening, retiring to cover during the day. Bongo normally fled immediately upon sensing human presence. When visiting water at the forest clearings, they entered cautiously and did not wallow
Last week March	Clouds of stable flies first noticed; Weakened yellow-backed duiker observed on road does not flee on approach by the researchers
April	<ol style="list-style-type: none"> 1. Clouds of stable flies first noticed on bongo 2. A solitary calf tormented by flies was observed wandering and vocalizing along road near Mombongo at mid-day 3. Two adult females and a juvenile at the Wali clearing were observed swimming in deep water for 1–2 min leaving only their heads exposed in an attempt to escape the flies 4. Bongos walk and rest along roads in Mombongo and safari area and do not flee when approached up to 10 m 5. Bongo sighted at Mbeli bai for the first time in history of study
May	<ol style="list-style-type: none"> 1. Solitary bongo (n = 6) covered by biting <i>Stomoxys</i> walk and rest on roads and in forest clearings in the Mombongo area during the hottest hours of day, wallowing in pools of water and vocalizing in torment. In each case, they were vigorously shaking their heads, dipping their ears in water in an attempt to elude the flies. One male was observed for over an hour in a clearing under the hot sun, until he fled, bellowing into the forest 2. Two adult male bongos standing in Mbeli clearing stream shaking heads nineteen times per minute dipping their ears in water, tail swatting, and vocalizing throughout the day over several days 3. One adult male at Mbeli disappears and later found dead nearby. Second male leaves the area
June	Flies decline and disappear. Bongo behaviour and flight distance appears to return to normal pre-March patterns: flight upon sensing human presence, activity predominantly crepuscular and nocturnal

Other species

In April–May, sitatunga at Mbeli, like bongo, spent nearly all daylight hours trying to deter the *Stomoxys*. Head-turning was performed repetitively, and ear and tail flicking sent sprays of water over their backs, but these methods seemed to do little more than brush some of the flies airborne for a few seconds.

All adult male sitatunga (n = 4) known to use Mbeli clearing disappeared during the fly outbreak and were never resighted. Two males appeared to lose weight during the fly-outbreak period prior to disappearing. In the following years, Mbeli recorded >4 new adult males visiting the clearing regularly (R. Parnell, pers. obs.). Adult female sitatunga (n = 5) behaviour also changed markedly, however, neither females nor juveniles were observed to lose condition and none died or disappeared. A newborn calf died during the fly outbreak.

Forest buffalo (*Syncerus caffer nanus*, Sparman) visiting Mbeli exhibited some discomfort and annoyance from the flies during April–May, however, they continued to use the areas regularly. Gorilla activity at Mbeli was low

during April and May. Gorilla use of the clearing returned to normal levels in June with gorillas regularly using the clearing (R. Parnell, unpubl. data). An adult female yellow-backed duiker (*Cephalophus silvicultor*, Afzelius) covered in *Stomoxys* flies was observed in extremely weak condition walking along the road near Mombongo.

Mortality observations

Seventeen bongos (eleven adult males, three adult females, two sub-adults and one juvenile) were found dead in the NNNP and Kabo FMU in late April and May 1997 (Fig. 2). Bongo carcasses were first observed in late April and the majority of animals died in early-mid May. Proximal cause of mortality included drowning (n = 4), vehicle collisions (n = 3), and bludgeoning by villagers with clubs (n = 1). Nine cases were categorized as uncertain. In contrast, we found only two bongo carcasses (leopard kills) during the rest of the 5-year study. Observations were recorded along roads, paths, and rivers regularly used by researchers and local communities, so any mortality in the area would

have been detected with similar probability over the course of the study.

Four yellow-backed duiker carcasses were found in southern Kabo forest in late April–May with two lying near pools of water on a road. Cause of death was uncertain.

Five bongo deaths associated with high fly numbers were reported in April–May from the Mondika area in Central African Republic c. 30 km north of Mombongo (C. Bocian, pers. comm.). At the Dzangha forest clearing in the Dzangha-Ndoki National Park (c. 65 km north), *Stomoxys* numbers were low and no mortality was reported (A. Turkalo, pers. comm.). Reports from the Lobeke area of Cameroon indicated high fly abundance and at least six cases of bongo mortality (H. Planton, pers. comm.). The location of carcasses and reports from Congo, Cameroon, and CAR suggest that *Stomoxys* flies caused bongo mortality over >2000 km².

Bongo abundance

Resighting histories from remote camera surveys registered an important bongo population decline, particularly in adult males, in association with the *Stomoxys* outbreak. During 1996–2001, a total of 83 adult males and 137 females were identified in the Kabo concession. Fifty-two

males were photographed during two camera trap surveys in late 1996 and early 1997 prior to the *Stomoxys* outbreak. In subsequent surveys (n = 11) during 1997–2001, only twelve males (23%) were resighted along with 31 newly sighted males. Conversely, 26 females (52%) identified prior to the outbreak were subsequently resighted along with 87 new females. Temporary movement away from the area during the high fly concentrations was noted. Three adult males from Mombongo were resighted 40–50 km southeast during and following the fly outbreak. Two of these males later moved back and were resighted in Mombongo.

Camera trap photo success rates also showed a marked decline in the abundance of adult male bongo in the Mombongo area following the outbreak (Fig. 4). Mean photographic rate for adult males prior to the outbreak was nearly ten times higher ($\bar{x} = 162$ photos/survey, n = 2, SD = 30) than during the following years ($\bar{x} = 18$, n = 11, SD = 8) (Mann–Whitney U-test, P = 0.018). In contrast, photo success rates for females, sub-adults, and calf cohorts before ($\bar{x} = 181$, n = 2, SD = 50) and after ($\bar{x} = 103$, n = 11, SD = 79) the fly outbreak were not significantly different (Mann–Whitney U-test, P = 0.19).

Bongo sign encounter rates along the Mombongo road showed similar drastic declines following the outbreak

Fig 4 Camera trap survey photo success rates for adult male bongo compared with females and young in the Mombongo area 1996–2001

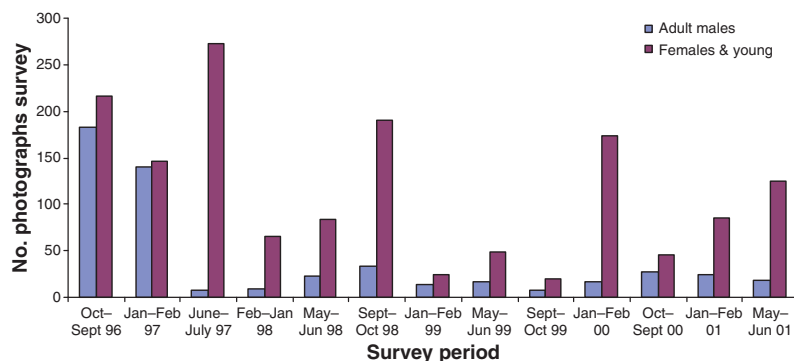
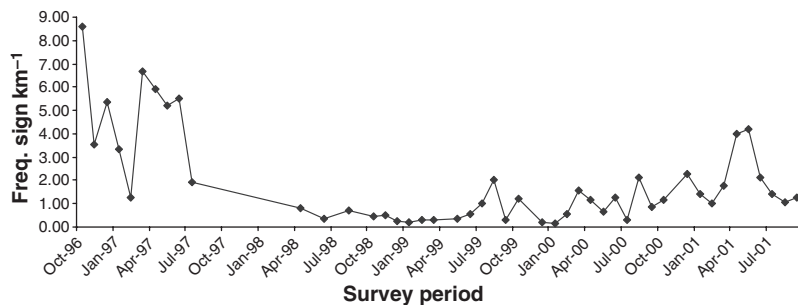


Fig 5 Bongo sign encountered on logging road surveys in the Mombongo area 1996–2001 (n = 16 km/survey)



(Fig. 5). Encounter rates decreased from 5.0 per km ($n = 8$, $SD = 2.18$) prior to the outbreak to 0.4 per km ($n = 9$, $SD = 0.19$) in the following year ($t_8 = 6.47$, $P = 0.0001$). A slight recovery trend was observed in the second ($n = 8$, $\bar{x} = 0.84$, $SD = 0.53$) ($t_8 = 2.78$, $P = 0.014$) and third years ($n = 8$, $\bar{x} = 0.9$, $SD = 1.23$) ($t_8 = 4.67$, $P = 0.001$). However, sign levels remained significantly lower than pre-outbreak levels ($t_8 = 6.51$, $P = 0.0001$) ($t_8 = 3.65$, $P = 0.004$).

Local community perceptions

Local hunters ($n = 10$ interviews) from Bomassa and Kabo villages reported that they were familiar with the two types of flies but had never observed them in such great numbers. They reported no previous knowledge of similar events and were surprised and concerned about the antelope mortalities.

Discussion

Environmental factors

Rainfall patterns in northern Republic of Congo in 1997 were similar to conditions reported for the outbreak in the Ngorongoro crater, Tanzania in 1962 (Fosbrooke, 1963). A prolonged severe dry season followed by exceptionally heavy rains created warm moist conditions that could have contributed to the development of several high abundance generations of *Stomoxys* flies. Similar to the Ngorongoro case, the fly outbreak in northern Congo was observed during a clearly marked period. Observations and interviews of local people in Congo suggest that *Stomoxys* outbreaks occurred annually in April–May; however, the lower fly numbers and shorter periods of the outbreaks did not noticeably increase mortality in wildlife.

Behaviour and mortality

Stomoxys are known to attack domestic horses and cattle causing anaemia, worry, and reduction of feeding time and efficiency (Radostits *et al.*, 2000). In northern Congo, the direct effects of the swarming biting flies and resulting attempts to fight-off the flies seem to have contributed to extreme fatigue, disruption of foraging patterns, modification of behaviour, and increased exposure to predation and accidents. Observations of bongo and examination of carcasses suggest that the physical torment and disruption

caused by the biting *Stomoxys* contributed directly to the deterioration of their condition. Veterinary examination of three culled bongo revealed no signs of disease. Signs of *Elaeophora sagitta*, a parasite commonly found in tragelaphine antelopes and buffalo, were observed in all three bongo and may have weakened the animals by interfering with cardiopulmonary circulation (Huchzermeyer, Penrith & Elkan, 2001). Our observations suggest that extreme fatigue and energy loss resulting from torment by biting flies increased bongo susceptibility to mortality. This would have been compounded by parasites and viral and bacterial infections.

The high number of bongo carcasses found compared with other species and direct observations of animal behaviour during that period suggest that bongos were the most severely affected species. Given the low probability of finding carcasses in dense forest habitat and rare frequency with which dead animals are normally encountered, actual mortality was thought to have been much higher than observed. Although only one sitatunga carcass was found, sitatungas are swamp and water specialists, and Mbeli was the only swamp habitat surveyed. Observations at Mbeli suggested that sitatungas were likely to have also been greatly negatively affected.

The *Stomoxys* outbreak occurred immediately after an exceptionally severe dry season when forage quality and energy levels would have been low, thus increasing the impact on bongo foraging patterns. The edge and forest clearing habitat preferences of bongo and sitatunga coincided with areas that would likely support high *Stomoxys* abundance (e.g. zones with warm, moist, decaying debris). The physiological and behavioural similarity between the two species in response to the flies suggests that *Stomoxys* preferred feeding on Tragelaphids in northern Congo. *Stomoxys*' preference for Tragelaphids has also been found in investigations in Kenya and Uganda (Mihok & Clausen, 1996).

Sex-related differences in energy reserves and expenditures may explain why mortality would have been higher for adult males than females in both bongo and sitatunga. This pattern is similar to die-offs of other highly polygamous ungulate species where intensive competition for mates has resulted in adult males having low energy reserves when entering a period of high environmental stress (Robinette *et al.*, 1957; Klein, 1968; Child, 1972; Coehlo, 1974; Frisch, 1984; Anderson, 1985; Clutton-Brock & Albon, 1985; Mkanda & Munthali, 1991). In these cases, females exhibit better resistance to extreme conditions.

Bongo distribution and abundance

The fly outbreak greatly affected local bongo distribution and abundance in the Kabo forest concession and perhaps a much greater area. The severity and extent of the local population decline suggests that such events, depending on their frequency and scale, could contribute significantly to limiting bongo abundance in Central Africa. Determining the extent of the bongo population decline in northern Congo may have been confounded by wide movement patterns and permanent emigration. However, mortality was observed over a large area and in two other large antelope species. Furthermore, camera trap surveys showed a high turnover of males. Each of the different data collection methods (photographic rates, re-sighting of individuals and sign surveys) as well as general observations indicate that the bongo population suffered a significant and abrupt decline over a broad area in association with the *Stomoxys* fly outbreak.

Conservation implications

Bongos occur in low densities or are absent in much of the lowland forest zone of Central Africa with localized patches of high abundance (Elkan, 2003). Conservation strategies should therefore incorporate redundancy in protecting populations to take into account potential vulnerability to *Stomoxys* outbreaks and local declines. Given the paucity of information on bongo population ecology, apparent widespread mortality, and the significant skewed mortality in adult males, there is a strong case for restriction, or suspension, of trophy hunting following population crashes related to *Stomoxys* outbreaks. In such cases, sustained trophy hunting pressure could potentially lead to decreased trophy quality, local extirpation of mature males, and longer term genetic effects on the population.

In management of safari hunting, quotas should be applied to entire population units; however, these units may be difficult to define. Hunting zones should be large and leased with long-term management objectives and obligations. Monitoring programs employing specimen and population structure data collection methods need to be implemented. Such regulation can provide the basis for sound management, increased transparency in the safari industry, adaptive feedback on the impact of hunting and detect natural population events, which may lead to a skewed sex ratio and decline in key game populations.

The die-off of large forest ungulates described here was a seemingly unusual and rare event. The relative lack of knowledge about forest mammals and difficulty in observing animals in lowland forest habitat, may contribute to under reporting of die-offs of even large-bodied mammals. This may account for local peoples' statements that they had not witnessed such mortality in the past. Understanding the nature, frequency and impact of such die-offs, and how they interact with other limiting factors (e.g. predation and hunting) are crucial to conservation and management of these species.

Acknowledgements

The Government of the Republic of Congo authorized and supported this investigation. Steve Blake, Sarah Elkan, David Morgan, Tomo Nishihara and the staff of the Mombongo research program contributed valuable field observations important to the documentation of the 1997 case. Sharon Deem, Francis Cuthbert, and David Garshelis provided helpful comments to improve this manuscript. Roger Moon shared information and references on *Stomoxys* ecology. Funding was provided by Wildlife Conservation Society, University of Minnesota Conservation Biology Program, Fulbright Foundation, Busch Gardens, Columbus Zoo, GEF-Congo, Mac Arthur Foundation, and Cincinnati Zoo.

References

- ANDERSON, J.L. (1985) Condition and related mortality in nyala (*Tragelaphus angasi*) in Zululand, South Africa. *J. Zool. Lond.* **207**, 37–380.
- CARBONE, C., CHRISTIE, S., CONFORTI, K., COULSON, T., FRANKLIN, N., GINSBERG, J.R., GRIFFITHS, M., HOLDENS, J., KAWANISHI, K., KINNNAIRD, M., LAIDLAW, R., LYNAM, A., MACDONALD, D.W., MARTYR, D., MCDUGAL, C., NATH, L., O'BRIEN, T., SEIDENSTICKER, J., SMITH, D.J.L., SUNQUIST, M., TILSON, R. & WAN SHAHRUDDIN, W.N. (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Anim. Conserv.* **4**, 75–79.
- CHILD, G. (1972) Observations on a wildebeest die-off in Botswana. *Arnoldia* **31**, 1–113.
- CLUTTON-BROCK, T.H. & ALBON, S.D. (1985) Competition and population regulation in social mammals. In: *Behavioral Ecology* (Eds. R. SIBLY and R. H. SMITH). Blackwell Scientific Publications, Oxford.
- COEHLO, A.M. (1974) Socio-bioenergetics and sexual dimorphism in primates. *Primates* **15**, 263–269.
- EAST, R. (1999) *African Antelope Database 1998*. Occasional Paper of the IUCN Species Survival Commission No. 21. IUCN, Gland, Switzerland and Cambridge, U.K.

- ELKAN, P.W. (2003) *Ecology and conservation of bongo antelope (Tragelaphus eurycerus) in lowland forest, northern Republic of Congo*. PhD thesis. University of Minnesota, St. Paul, MN, U.S.A.
- ERB, J.D. & BOYCE, M.S. (1999) Distribution of population declines in large mammals. *Conserv. Biol.* **13**, 199–201.
- FAY, M., AGNAGNA, M. & MOUTSAMBOTE, J.M. (1990) *Surveys of the Nouabale-Ndoki Region, Northern Congo*. Wildlife Conservation Society, Bronx, N.Y.
- FOSBROOKE, H.A. (1963) The *Stomoxys* plague in Ngorongoro, 1962. *E. Afr. Wildl. J.* **1**, 124–126.
- FRISCH, R.E. (1984) Body fat, puberty, and fertility. *Biol. Rev.* **59**, 161–188.
- HILLMAN, J.C. (1986) Aspects of the biology of the bongo antelope *Tragelaphus euryceros* (Ogilby 1837) in the southwest Sudan. *Biol. Conserv.* **38**, 255–272.
- HUCHZERMAYER, F.W., PENRITH, M.L. & ELKAN, P.W. (2001) Multifactorial mortality in bongos and other wild ungulates in the north of the Congo Republic. *Ond. J. Vet. Med.* **68**, 263–269.
- KINGDON, J. (1982) *East African Mammals: An Atlas of Evolution in Africa*. IIC Bovids. Academic Press, London.
- KINGDON, J. (1997) *Field Guide to African Mammals*. Academic Press, London.
- KLEIN, D.R. (1968) The introduction, increase, and crash of reindeer on St. Mathew island. *J. Wildl. Manage.* **32**, 350–367.
- KUNZ, S.E. & MONTY, J. (1976) Biology and ecology of *Stomoxys nigra* Macquart and *Stomoxys calcitrans* (L.) (Diptera, Muscidae) in Mauritius. *Bull. Entomol. Res.* **66**, 745–755.
- LETOUZEY, R. (1968) *Etude Phytogéographique du Cameroun*. Encyclopedie Biologique. Editions Paul Lechevalier, Paris.
- MIHOK, S. & CLAUSEN, P.H. (1996) Feeding habits of *Stomoxys* spp. stable flies in a Kenyan forest. *J. Med. Vet. Entomol.* **10**, 392–394.
- MKANDA, F.X. & MUNTHALI, S.M. (1991) Causes of mortality of nyala (*Tragelaphus anagasi* Gray) in Lengwe National Park, Malawi. *Afr. J. Ecol.* **29**, 28–36.
- RADOSTITS, O.M., GAY, C.C., BLOOD, D.C. & HINCHCLIFF, K.W. (2000) Diseases caused by arthropod parasites. In: *Veterinary Internal Medicine*, 6th edn (Eds. S. J. ETTINGER and E. C. FELDMAN). WB Saunders, Philadelphia, PA.
- RALLS, K. (1978) *Tragelaphus eurycerus*. *Mammal. Species* **111**, 1–4.
- ROBINETTE, W.L., GASHWILER, J.S., LOW, J.B. & JONES, D.A. (1957) Differential mortality by sex and age of mule deer. *J. Wildl. Manage.* **21**, 1–16.
- WHITE, L. & EDWARDS, A. (2000) Methods for assessing the status of animal populations. In: *Conservation Research in the African Rain Forests: A Technical Handbook*. (Eds L. WHITE and A. EDWARDS). Wildlife Conservation Society, New York.
- YOUNG, T. (1994) Natural die-offs of large mammals: implications for conservation. *Conserv. Biol.* **8**, 410–418.
- YOUNG, T. (1999) Catastrophes are still interesting. *Conserv. Biol.* **13**, 202.
- ZUMPF, F. (1973) *The Stomoxysine Biting Flies of the World. Diptera: Muscidae. Taxonomy, Biology, Economic Importance and Control Measures*. Gustav Fischer, Stuttgart.

(Manuscript accepted 1 April 2008)

doi: 10.1111/j.1365-2028.2008.00980.x